SYSTEMATIC FOLIAR MORPHOLOGY OF PHYLLANTHOIDEAE (EUPHORBIACEAE). I. CONSPECTUS[1]

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ABSTRACT

Leaf architecture and epidermal morphology of 259 species representing 51 genera in the Phyllanthoideae (Euphorbiaceae) vary in a taxonomically significant way. Most tribes are relatively homogeneous and well defined, with most exceptions being tribes containing herbaceous or highly xerophytic genera. Tribes that are generally considered to be closely related have similar leaves. Increase in venational organization correlates with specialization in floral morphology. Foliar morphology also indicates genera whose relationships warrant reconsideration, particularly *Celianella, Croizatia, Didymocistus, Jablonskia, Neowawraea,* and *Uapaca.* Theoid teeth and incipient or vestigial actinodromy support placement of Euphorbiaceae near the Violales in the Dilleniidae, rather than in the Rosidae.

Paleobotanists, faced with the task of identifying fossil angiosperms in the absence of megafossils of reproductive parts, have instead depended on the morphology and anatomy of vegetative structures, especially leaves. The last three decades have seen a tremendous increase in the sophistication of the techniques for investigation and description of foliar morphology (review by Dilcher, 1974; see also Fryns-Claessens & van Cotthem, 1973; Hickey, 1973; Hill, 1980; Payne, 1979; Stace, 1965). Particularly important in this progress was Hickey's (1973) development of a precise and non-overlapping terminology for the description of dicotyledonous leaf architecture, defined by Hickey as "the placement and form of those elements constituting the outward expression of leaf structure, including venation patterns, marginal configuration, leaf shape, and gland position."

Taxonomists studying higher taxa of extant angiosperms have generally ignored foliar characters, particularly aspects of architecture. Yet Hickey and Wolfe (1975), in their pioneering survey of dicotyledon leaves, found "coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships" at the ordinal and subclass levels. A few other studies have demonstrated higher systematic value in leaf architecture, notably in the Hamamelididae (Wolfe, 1973), Onagraceae (Hickey, 1980), Marcgraviaceae (Bedell, 1981), Rubiaceae (Pray, 1953), and Rutaceae (Dede, 1962). Clearly, however, the leaf architecture of extant angiosperms remains largely unexplored by systematists.

Cuticular characters have had a longer history of use in taxonomic investigations (see review by Stace, 1965), although here, too, our knowledge of fossil cuticle may exceed what we know of extant angiosperms. Epidermal features have proven systematically useful in several dicotyledonous families, including, among others, the Celastraceae (Den Hartog & Baas, 1978), Euphorbiaceae (Raju & Rao, 1977), and Magnoliaceae and related families (Baranova, 1972).

The Euphorbiaceae are an ideal family with which to explore the potential contribution of leaf architecture and epidermal morphology to higher level taxonomy. This large family, which contains about 300 genera and 7,000 species (Webster, 1967), has long attracted systematists' attention, resulting in an impressive series of infrafamilial classifications. The first treatment, by Jussieu (1824), has been succeeded by further treatments prepared by Baillon (1858), Mueller (1866), Bentham (1880), Pax (1890), Pax and Hoffmann (1931), Hurusawa (1954), and Hutchinson (1969). In addition to the information on floral morphology on which these systems are largely based, evidence has accumulated on anat-

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omy (Rothdauscher, 1896; Gaucher, 1902; Pax & Hoffman, 1931; Metcalfe & Chalk, 1950: 1207–1235; Hayden, 1980), palynology (Erdtman, 1952: 165–175; Punt, 1962; Köhler, 1965), and cytology (Webster & Ellis, 1962; Miller & Webster, 1966). Webster (1975) produced a treatment taking into account data from all these fields. Yet, in spite of all this attention, the foliar morphology of the Euphorbiaceae remains little known (but see Sehgal & Paliwal, 1974; Hayden, 1980).

The phylogenetic relationships of the Euphorbiaceae are controversial, which also makes the study of euphorbiaceous leaf architecture potentially valuable. There are two schools of thought regarding the position of the family. The first has accepted rosid affinities. Based on the plurilocular gynoecium containing two (or one) ovules in each locule and the presence of a nectary disk, Cronquist (1981) argued for a close relationship to the Celastrales. Webster (1967) was much more cautious, suggesting that Euphorbiaceae evolved from a primitive rosalean plexus. Among living orders, he considered the Euphorbiaceae closest to the Geraniales, with which they share a similar gynoecium and epitropous ovules. The second school has placed the Euphorbiaceae in the Dilleniidae near the Violales and Malvales (Croizat, 1940; Hickey & Wolfe, 1975; Takhtajan, 1980; Thorne, 1976). These authors emphasized the similarities between the wood, leaves, gynoecium, and pollen of the Euphorbiaceae and the primitive members of these orders, particularly the Flacourtiaceae and Sterculiaceae. A few others, including Hutchinson (1969) and Airy Shaw (1965, 1973) have proposed that the family is polyphyletic, with relatives among both the rosids and dilleniids.

In order to examine the systematic value of foliar morphology in general and to try to shed some light on the relationships of the Euphorbiaceae, I chose to work with the Phyllanthoideae, which is generally recognized to be the most primitive subfamily because many of its members have petaliferous flowers that, although unisexual, contain large androecial or gynoecial rudiments. This subfamily of 57 genera and about 2,000 species can be recognized by its lack of latex; alternate, stipulate leaves; tricolporate to porate, non-spinose pollen; biovulate locules; and ecarunculate seeds. In this paper I will describe phyllanthoid foliar morphology and discuss its bearing on the ancestry of the Euphorbiaceae. In later papers (Levin, 1986 and in press) I will present results of phenetic and cladistic analyses of the leaf characters that demonstrate that they do vary in taxonomically and phylogenetically meaningful ways.

MATERIALS AND METHODS

I examined leaves of 259 species belonging to 49 genera that Webster (1975) included in the Phyllanthoideae. I was unable to obtain leaves of *Apodiscus* Hutch., *Chascotheca* Urb., *Chorisandrachne* Airy Shaw, *Danguyodrypetes* Leandr., *Gonatogyne* Muell. Arg., *Oreoporanthera* Hutch., *Pleiostemon* Sond., and *Securinega* sensu stricto. I also studied leaves from *Martretia* and *Paradrypetes*, genera that are usually included in the Phyllanthoideae but were excluded by Webster. For all but the very largest genera (e.g., *Glochidion* and *Phyllanthus*), my sample includes a minimum of 10% of the species.

Leaves were removed from herbarium specimens and cleared and stained according to the method of Wolfe (cited in Dilcher, 1974), except that some were mounted in Eukitt rather than Permount. Most were photographed with Kodak Technical Pan Film SO-115, a black-and-white, panchromatic negative film with extended red sensitivity, which was then developed and printed for maximum contrast. The resulting prints frequently showed details of venation more clearly than the original cleared leaves. Additional photomicrographs were taken with Kodak Panatomic-X, often using a green filter to enhance contrast. Cleared leaves and negatives are stored in the collections of Dr. Jack Wolfe, United States Geological Survey, Denver, Colorado, and the current author. Specimens and their vouchers are listed below with the descriptions of their respective genera. Because each species was rarely represented by more than a few cleared leaves from a single individual, I generally checked architectural characters on additional specimens of the same or closely related species. Whenever possible, herbarium specimens that had been annotated by authorities were chosen. In a few cases, I checked suspected determinations using the appropriate regional manuals or monographs.

Initially, each species was scored individually. I then grouped species into homogeneous groups. Most of these groups correspond to genera, subgenera, or sections, following Pax and Hoffmann (1922) for most genera, Jablonsky (1915) for *Bridelia* and *Cleistanthus*, and more recent monographs when these were available. In a few cases (e.g., *Bridelia*, *Drypetes*) the species within a section formed two or more homogeneous groups, one or more of which was highly similar in architectural and epidermal characters to groups belonging to other sections. In these cases I disregarded the taxonomy and lumped similar species into a single group. Following the terminology of numerical taxonomists, I will refer to the homogeneous groups as operational taxonomic groups, or OTUs, in this and future papers (Levin, 1986 and in press). Table 1 lists the OTUs included in this study.

CHARACTERS

Leaf architectural terminology generally follows Hickey (1971, 1973). Leaf size classes are those of Raunkiaer (1934); nothing about venation is implied by the terms microphyll or megaphyll. Terminology for cuticular characters generally follows Dilcher (1974), who systematized Stace's (1965) terms. Specific trichome types follow Payne (1977) and stomatal terminology includes terms introduced by Payne (1970, 1979). I also recorded a few features of the leaf's internal anatomy, including type and distribution of crystals, degree and extent of sclerification of the bundle sheath, size of the terminal tracheids relative to the other tracheary elements in the freely-ending veinlets, and prominent idioblasts.

A few characters that I scored exhibited considerable variation within groups that were otherwise homogeneous. These characters include size and shape of the leaf, shape of the apex and base (with the exception of base balance), relative size of the terminal tracheids, sclerification of the bundle sheath, ultimate marginal venation, epidermal cell size, and trichome density. The last three of these have been shown in other groups to be sensitive to the environmental conditions under which the leaf developed (Stace, 1965; Sharma & Dunn, 1969; Lucic, 1970; Ehleringer & Bjorkman, 1978); such phenotypic plasticity would be particularly troublesome with small sample sizes such as mine. Marginal venation and sclerification of the bundle sheath can also show evolutionary instability, at least in the Magnoliaceae (Tucker, 1977) and *Hibbertia* (Rury & Dickison, 1977). Leaf shape characters are frequently used in keys to species in the Phyllanthoideae, suggesting that shape varies considerably at the species level, possibly in response to interspecific ecological differences, and thus will not be useful at higher taxonomic levels.

When I eliminated those characters that varied too much or that were monomorphic within the Phyllanthoideae, 43 characters remained. The character states for these characters and their codes are listed in Table 2. The order of character states within a character does not necessarily imply any evolutionary sequence. The following characters require more explanation:

3. Margin. In most members of the Aporuseae, the margins are entire to crenulate with small glands in the sinuses (Figs. 64–67). See the descriptions of this tribe for more details of this condition, which I recorded as state G. Three genera, *Bischofia, Drypetes,* and *Putranjiva,* bear theoid teeth. See the descriptions of these genera for a more thorough discussion of the tooth morphology.

4. Venation. I recognized two expressions of brochidodromous venation. In the first, state B, the secondary loop ends abruptly and, if it is accompanied by outer loops, these are formed by well differentiated secondary, tertiary, and quaternary veins (Figs. 32, 34). In the second, state W, the secondary loop is accompanied by additional secondary loops that gradually decrease in size and merge into tertiary loops (Figs. 31, 36, 97), a pattern I will refer to as weakly brochidodromous. This pattern differs from eucamptodromy (state U) in that in the latter the connections between one secondary and its superadjacent secondary are not formed by prominent secondary loops but are simply higher order crossveins (Figs. 41, 44). In the Phyllanthoideae, weak brochidodromy may form the evolutionary link between eucamptodromy and simple brochidodromy.

7. Angle of origin of basal secondary. If the angle formed between the lowermost pair of secondary veins and the midrib was consistent with the angles formed by the other lower secondaries (Figs. 14, 36, 97), I recorded state S; if the basal angle was either markedly more acute (Figs. 55, 64) or more obtuse (Figs. 3, 62), I recorded states A or O, respectively.

12. Size of outer loops. The sizes of the loops, if any, accompanying a secondary loop may be uniform (Fig. 90), decrease upward from the secondary loop (Fig. 55), or vary irregularly (Figs. 90, 119).

17. Composite intersecondary frequency. The three classes I recognized appear to have well marked boundaries in the Phyllanthoideae.

18. Intramarginal vein. In some sections of *Bridelia* the outer portions of the secondary loops form a vein at the leaf margin (Figs. 37, 38).

TABLE 1. Character states of taxa studied. Sequence of genera follows Webster (1975). Two genera that were examined, *Poranthera* and *Reverchonia*, are not included in the table because their extremely xeromorphic leaves provided few characters; they are described in full in the text. See Table 2 and text (pp. 30, 39) for explanation of character states. Numbers in parentheses refer to operational taxonomic units (OTUs) used in numerical analyses published elsewhere (Levin, 1986 and in press).

	Wielandia (1)	*Astrocasia* (2)	*Blotia* (9)	*Discocarpus* (5)	*Heywoodia* (3)	*Lachnostylis* (4)	*Pentabrachium* (13)	*Petalodiscus* (8)	*Savia* § *Heterosavia* (6)	*S.* § *Savia* (7)	*Amanoa* (10)	*Actephila* group 1 (11)	*Actephila* group 2 (12)	*Croizatia* (93)	*Bridelia* group 1 (14)	*Bridelia* group 2 (15)	*Bridelia* group 3 (16)	*Cleistanthus acuminatissimus* (17)	*C.* § *Stipulati* (18)	*C.* group 3 (19)	*C.* § *Chartacei* (20)	*C.* § *Cleistanthus* (21)	*C. saichikii* (22)	*C.* § *Australes* (23)	*C.* § *Leiopyxis* (24)	*Dicoelia* (25)	*Andrachne* group 1 (26)	*A.* § *Phyllanthopsis* (27)	*Spondianthus* (28)	*Antidesma* group 1 (29)	*A.* group 2 (30)	*A.* § *Tetrandra* (31)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
2. Basal balance	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
4. Venation	B	B	B	B	B	B	U	B	B	B	B	B	W	B	W	U	B	W	W	U	B	U	W	B	W	W	B	B	B	W	W	B
5. Primary size	m	m	m	m	m	S	m	m	m	m	m	S	m	m	S	S	S	S	S	S	S	S	m	S	m	m	S	m	m	m	m	S
6. 2° angle	M	M	W	M	M	M	M	M	M	M	M	W	M	W	M	M	M	M	M	N	W	N	M	W	M	M	N	N	M	M	M	M
7. Angle, basal 2°	S	O	S	S	A	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	A	S	A
8. Angle, lower 2°	S	S	A	S	S	S	A	A	S	S	S	S	S	A	O	O	O	O	S	S	S	S	S	S	S	A	O	S	S	S	S	S
9. Angle, upper 2°	S	O	S	S	O	S	S	S	S	S	S	S	S	S	S	A	A	O	O	O	S	O	O	S	O	S	S	S	S	S	S	S
10. 2° course	A	A	A	A	U	A	U	A	A	A	A	A	A	A	A	U	U	A	A	U	A	U	A	A	A	U	A	A	A	A	A	A
11. 2° loop angle	A	A	O	R	R	A	O	R	R	A	A	A	A	R	A	O	O	R	R	R	R	R	R	R	R	R	A	A	R	R	R	R
12. Outer loop size	U	U	U	U	U	U	D	U	U	U	D	D	D	U	D	A	A	D	D	D	U	D	D	U	D	D	D	I	D	D	D	U
13. 3° angle, admedial	A	R	R	A	R	A	R	R	A	A	O	R	R	A	R	R	R	A	R	R	R	O	R	R	R	R	R	R	R	R	R	R
14. 3° angle, exmedial	R	R	R	R	R	R	A	R	R	R	A	R	R	R	R	R	R	R	R	R	R	R	R	R	R	A	A	R	R	A	A	A
15. 3° pattern	R	W	O	W	R	R	W	O	O	O	R	R	p	W	p	p	p	p	p	W	W	W	W	O	W	p	W	W	R	W	W	O
16. Simple intersecond.	—	—	+	—	+	—	—	—	+	+	+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17. Composite intersecond.	F	A	I	I	A	A	A	F	A	I	I	F	I	A	A	A	A	A	A	A	A	A	A	A	A	A	A	I	A	A	A	A
18. Intramarginal vein	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19. High order pattern	R	o	o	O	o	R	O	O	R	O	r	R	R	o	o	O	O	O	O	O	o	O	O	R	R	O	o	r	R	o	o	o
20. High order, size	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
21. Highest order present	5	6	6	5	5	6	6	5	5	5	6	5	5	5	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5

TABLE 1. Continued.

	Wielandia (1)	*Astrocasia* (2)	*Blotia* (9)	*Discocarpus* (5)	*Heywoodia* (3)	*Lachnostylis* (4)	*Pentabrachium* (13)	*Petalodiscus* (8)	*Savia* § *Heterosavia* (6)	*S.* § *Savia* (7)	*Amanoa* (10)	*Actephila* group 1 (11)	*Actephila* group 2 (12)	*Croizatia* (93)	*Bridelia* group 1 (14)	*Bridelia* group 2 (15)	*Bridelia* group 3 (16)	*Cleistanthus acuminatissimus* (17)	*C.* § *Stipulati* (18)	*C.* group 3 (19)	*C.* § *Chartacei* (20)	*C.* § *Cleistanthus* (21)	*C. saichikii* (22)	*C.* § *Australes* (23)	*C.* § *Leiopyxis* (24)	*Dicoelia* (25)	*Andrachne* group 1 (26)	*A.* § *Phyllanthopsis* (27)	*Spondianthus* (28)	*Antidesma* group 1 (29)	*A.* group 2 (30)	*A.* § *Tetrandra* (31)
22. Areole development	I	I	D	D	I	D	I	D	I	D	I	I	I	I	I	I	I	I	I	I	I	I	D	I	I	I	I	I	I	I	I	I
23. Areole arrangement	R	R	R	O	R	R	R	O	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. Areole shape	I	I	R	R	I	I	I	R	I	R	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I	I	I	I	I	I	I	I
25. Areole size	M	M	M	S	M	M	M	M	M	M	M	M	M	M	M	M	S	M	M	M	L	M	M	M	S	M	M	S	M	M	M	M
26. Veinlets	2	2	S	A	3	2	2	S	2	S	3	2	2	2	2	2	S	2	2	2	2	2	2	2	2	2	S	S	2	2	2	2
27. Prismatic, mesophyll	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
28. Prismatic, veins	+	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	+	–	+	+	–	+	–	+	–	–	–	–	–	–	–	–
29. Druses, mesophyll	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30. Druses, veins	–	+	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
31. Epidermal wall, adaxial	S	S	S	U	S	S	U	S	S	S	S	U	U	S	S	S	S	U	U	U	S	U	U	U	U	U	U	U	S	U	U	U
32. Epidermal wall, abaxial	S	S	S	U	S	S	U	S	S	S	S	U	U	S	S	S	S	U	U	U	S	U	U	U	U	U	U	U	S	U	U	U
33. Epidermal papillae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
34. Stomatal location	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	b	L	L	L	L	L	L	L	L	L	L
35. Stomatal index	B	B	C	C	B	C	B	C	C	C	B	B	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	P	P	P	P	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	A	A	P	P	P	P
37. Water stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
38. Unicellular trichomes	A	A	A	A	A	A	S	A	A	A	A	A	S	S	A	A	A	S	S	S	S	A	A	A	A	S	S	S	A	S	S	S
39. Multicellular trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40. Peltate trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41. Filiform sclereids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	+	–	–	–	–	–	–
42. Tannin. epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+
43. Sclerified epidermal cells	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 1. Continued.

	A. § *Montana* (32)	*A.* § *Velutinosa* (33)	*A.* § *Ghaesembilla* (34)	*Celianella* (35)	*Hyeronima* (36)	*Leptonema* (37)	*Thecacoris* (38)	*Aporusa* (39)	*Ashtonia* (40)	*Baccaurea* group 1 (41)	*B.* § *Pierardia* (42)	*B. Dubiae* (43)	*B.* § *Isoandrion* (44)	*Didymocistus* (45)	*Maesobotrya* (46)	*Protomegabaria* (47)	*Richeria* (48)	*Drypetes* group 1 (49)	*D.* group 2 (50)	*D.* group 3 (51)	*D.* group 4 (52)	*D.* group 5 (53)	*D.* group 6 (54)	*Neowawraea* (90)	*Putranjiva* (55)	*Jablonskia* (56)	*Keayodendron* (57)	*Lingelsheimia* (94)	*Meineckia* (58)	*Pseudolachnostylis* (59)	*Zimmermannia* (60)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
2. Basal balance	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	A	A	A	A	A	S	A	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	G	G	G	G	G	G	E	G	E	G	T	T	E	T	T	T	E	T	E	E	E	E	E	E
4. Venation	B	W	W	B	W	B	B	B	B	W	W	B	B	W	W	W	W	B	W	U	B	B	B	W	B	B	B	B	B	B	B
5. Primary size	m	m	S	M	S	m	S	S	S	S	S	S	S	m	S	S	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m
6. 2° angle	M	M	M	N	M	N	M	M	M	M	M	N	W	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	N	M	M
7. Angle, basal 2°	A	A	O	S	S	O	S	A	A	O	A	S	A	S	A	S	S	A	A	A	A	A	A	S	A	S	S	S	S	S	S
8. Angle, lower 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	S	S	S	O	S
9. Angle, upper 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	S	O	S	S	S	S	O
10. 2° course	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	U	A	A	A	A	A	A	A	A	A	A	A
11. 2° loop angle	R	R	R	R	A	R	R	A	A	R	A	O	R	R	A	A	R	R	R	R	R	R	R	A	A	R	R	A	R	A	A
12. Outer loop size	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	U	D	A	U	U	U	D	U	U	U	D	D	D	D
13. 3° angle, admedial	R	R	R	R	R	R	R	R	R	R	O	R	R	R	R	O	R	R	R	R	R	R	R	R	O	R	R	R	R	R	R
14. 3° angle, exmedial	A	A	A	R	A	A	A	A	A	A	A	R	A	A	A	A	A	R	R	R	R	R	R	A	A	R	R	A	A	R	A
15. 3° pattern	O	W	W	W	W	W	O	W	W	p	P	W	W	p	p	p	W	O	O	W	O	r	O	p	O	O	O	W	W	W	W
16. Simple intersecond.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17. Composite intersecond.	A	A	A	I	A	A	A	I	I	A	A	A	A	A	A	A	I	I	I	I	I	A	I	I	I	A	F	A	A	A	A
18. Intramarginal vein	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19. High order pattern	o	o	o	R	o	o	o	o	o	o	r	o	o	O	o	o	o	o	o	O	o	r	O	O	o	o	R	o	R	O	o
20. High order, size	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	m	M	M
21. Highest order present	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6	5	4	5	6	5	5	5	5	4	5	5

TABLE 1. Continued.

	A. § *Montana* (32)	*A.* § *Velutinosa* (33)	*A.* § *Ghaesembilla* (34)	*Celianella* (35)	*Hyeronima* (36)	*Leptonema* (37)	*Thecacoris* (38)	*Aporusa* (39)	*Ashtonia* (40)	*Baccaurea* group 1 (41)	*B.* § *Pierardia* (42)	*B. Dubiae* (43)	*B.* § *Isoandrion* (44)	*Didymocistus* (45)	*Maesobotrya* (46)	*Protomegabaria* (47)	*Richeria* (48)	*Drypetes* group 1 (49)	*D.* group 2 (50)	*D.* group 3 (51)	*D.* group 4 (52)	*D.* group 5 (53)	*D.* group 6 (54)	*Neowawraea* (90)	*Putranjiva* (55)	*Jablonskia* (56)	*Keayodendron* (57)	*Lingelsheimia* (94)	*Meineckia* (58)	*Pseudolachnostylis* (59)	*Zimmermannia* (60)
22. Areole development	I	I	D	I	I	I	I	I	I	I	i	I	i	D	i	I	I	I	I	D	I	i	D	D	I	I	I	I	I	D	I
23. Areole arrangement	R	R	R	R	R	R	R	R	R	R	R	R	R	O	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	O	R
24. Areole shape	I	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I	I	I	I	I	R	I	R	R	I	I	I	I	I	R	I
25. Areole size	M	M	S	M	M	M	M	M	M	M	L	M	M	S	M	M	M	M	M	M	L	L	S	S	M	M	M	M	M	S	M
26. Veinlets	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	S	2	2	2	2	2	2	S	2
27. Prismatic, mesophyll	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–	–	–
28. Prismatic, veins	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	–	–	–	–	–	–
29. Druses, mesophyll	–	–	–	–	–	–	–	+	–	+	+	+	+	–	+	–	+	+	–	–	–	–	–	–	–	–	+	+	–	–	–
30. Druses, veins	–	–	–	–	–	–	–	+	–	+	+	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	+	+	–	+	–
31. Epidermal wall, adaxial	U	U	U	S	S	S	U	S	S	S	U	U	S	S	S	S	S	U	U	U	U	U	U	S	S	S	S	S	U	S	S
32. Epidermal wall, abaxial	U	U	U	S	S	S	U	S	S	S	U	U	U	S	U	S	S	U	U	U	U	U	U	S	S	S	S	S	U	S	S
33. Epidermal papillae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–
34. Stomatal location	L	L	b	L	L	B	L	L	L	L	L	L	L	L	L	b	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
35. Stomatal index	B	B	C	C	B	C	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	A	A	A	A	A	A	P	A	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P
37. Water stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38. Unicellular trichomes	S	S	S	A	A	S	S	S	S	T	A	S	S	T	S	S	S	A	A	A	A	A	A	A	A	A	S	A	A	S	A
39. Multicellular trichomes	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40. Peltate trichomes	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41. Filiform sclereids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42. Tannin. epidermal cells	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
43. Sclerified epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 1. Continued.

	Flueggea (16)	*Breynia* (62)	*Glochidion* § *Glochidion* (63)	*G.* group 2 (64)	*G.* group 3 (65)	*Margaritaria* (67)	*Phyllanthus* § *Adenoglochidion* (68)	*P.* § *Anisonema* (69)	*P.* § *Aporosella* (70)	*P.* § *Cicca* (71)	*P.* § *Eleutherogynium* (72)	*P.* § *Emblica* (73)	*P.* § *Floribundi* (74)	*P.* subg. *Gomphidium*, group 1 (75)	*P.* subg. *Gomphidium*, group 2 (76)	*P.* § *Hemicicca* (77)	*P.* § *Heteroglochidion* (78)	*P.* § *Nothoclema* (79)	*P.* § *Nymphanthus* (80)	*P.* § *Paragomphidium* (81)	*P.* § *Phyllanthodendron* (82)	*P.* § *Polyandroglochidion* (83)	*P.* § *Psychoglochidion* (84)	*P.* § *Scepasma* (85)	*Richeriella* (86)	*Sauropus* (87)	*Synostemon* (66)	*Uapaca* (88)	*Hymenocardia* (89)	*Bischofia* (91)	*Martretia* (92)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	C	S
2. Basal balance	S	S	S	S	A	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	S	S	A	S	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	T	E
4. Venation	W	W	W	W	W	B	B	W	W	W	B	W	B	B	B	W	B	W	W	B	W	B	B	B	B	W	W	U	W	B	B
5. Primary size	m	m	S	S	S	m	m	m	m	m	m	S	S	S	S	m	m	m	m	S	m	m	m	m	m	m	m	S	S	m	S
6. 2° angle	M	M	M	M	M	M	M	M	M	M	N	N	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
7. Angle, basal 2°	S	S	S	S	S	S	S	S	S	O	O	O	S	O	S	S	S	S	O	O	S	S	S	S	S	S	S	S	A	S	S
8. Angle, lower 2°	S	O	O	A	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A
9. Angle, upper 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	O	S	S	S	A	S
10. 2° course	A	A	A	A	A	A	A	A	A	A	A	U	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
11. 2° loop angle	A	A	A	A	A	A	A	A	A	A	A	O	R	A	A	A	O	A	A	A	A	O	A	O	R	R	A	A	R	A	O
12. Outer loop size	D	D	D	D	D	U	U	D	D	D	U	D	U	U	I	D	U	D	D	U	D	I	U	I	U	D	D	A	D	U	I
13. 3° angle, admedial	R	O	R	R	R	R	R	R	R	R	R	A	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	O
14. 3° angle, exmedial	R	A	R	R	A	R	A	A	A	A	R	A	A	A	R	A	R	A	A	A	A	R	A	R	A	A	R	A	R	A	R
15. 3° pattern	p	p	P	p	P	W	O	W	W	W	R	R	W	W	R	W	W	W	O	R	p	r	W	R	W	p	R	p	W	R	O
16. Simple intersecond.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17. Composite intersecond.	A	A	A	A	A	I	A	F	F	F	A	F	I	I	A	I	I	I	F	A	I	A	F	A	F	I	A	I	A	A	F
18. Intramarginal vein	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19. High order pattern	o	o	o	o	o	o	o	o	o	o	R	R	R	o	R	R	R	o	R	R	o	r	o	o	o	o	R	o	O	R	R
20. High order, size	M	M	M	M	M	M	M	M	M	M	h	M	M	M	h	M	M	M	M	h	M	M	M	M	M	M	F	M	M	M	M
21. Highest order present	5	5	5	5	5	5	6	5	6	5	5	5	5	5	4	5	5	5	5	5	5	4	5	4	5	6	4	5	6	5	5

TABLE 1. Continued.

	Flueggea (16)	*Breynia* (62)	*Glochidion* § *Glochidion* (63)	*G.* group 2 (64)	*G.* group 3 (65)	*Margaritaria* (67)	*Phyllanthus* § *Adenoglochidion* (68)	*P.* § *Anisonema* (69)	*P.* § *Aporosella* (70)	*P.* § *Cicca* (71)	*P.* § *Eleutherogynium* (72)	*P.* § *Emblica* (73)	*P.* § *Floribundi* (74)	*P.* subg. *Gomphidium*, group 1 (75)	*P.* subg. *Gomphidium*, group 2 (76)	*P.* § *Hemicicca* (77)	*P.* § *Heteroglochidion* (78)	*P.* § *Nothoclema* (79)	*P.* § *Nymphanthus* (80)	*P.* § *Paragomphidium* (81)	*P.* § *Phyllanthodendron* (82)	*P.* § *Polyandroglochidion* (83)	*P.* § *Psychoglochidion* (84)	*P.* § *Scepasma* (85)	*Richeriella* (86)	*Sauropus* (87)	*Synostemon* (66)	*Uapaca* (88)	*Hymenocardia* (89)	*Bischofia* (91)	*Martretia* (92)
22. Areole development	I	I	I	I	I	I	I	I	I	I	I	I	I	I	i	I	I	I	I	I	I	i	I	I	I	I	I	I	D	i	I
23. Areole arrangement	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. Areole shape	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I
25. Areole size	S	M	M	M	M	S	M	S	S	S	M	S	S	M	M	M	M	S	M	M	M	M	M	S	M	S	S	M	S	M	M
26. Veinlets	2	2	2	2	2	2	2	2	2	2	2	S	2	2	2	S	2	2	2	2	2	2	3	2	2	2	S	2	2	2	2
27. Prismatic, mesophyll	−	−	−	−	−	−	−	+	−	−	+	−	+	−	+	−	+	+	−	−	−	−	+	−	−	−	−	−	−	−	−
28. Prismatic, veins	−	−	−	−	−	−	−	+	+	−	+	−	+	−	+	−	+	+	−	−	−	+	+	−	−	−	−	−	+	−	−
29. Druses, mesophyll	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−
30. Druses, veins	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	+
31. Epidermal wall, adaxial	S	U	S	S	S	S	S	S	S	S	S	S	S	S	U	U	S	S	S	S	U	S	S	S	S	U	S	S	S	S	U
32. Epidermal wall, abaxial	S	U	U	U	U	S	S	S	S	S	S	S	S	S	U	U	S	S	S	S	S	S	U	S	S	U	U	S	S	S	U
33. Epidermal papillae	+	+	−	−	+	+	−	−	−	−	−	−	−	+	+	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−
34. Stomatal location	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	B	L	L	L	b
35. Stomatal index	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	A	P	P	P
37. Water stomata	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
38. Unicellular trichomes	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	S	S	A	A
39. Multicellular trichomes	−	+	+	+	+	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−
40. Peltate trichomes	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
41. Filiform sclereids	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
42. Tannin. epidermal cells	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
43. Sclerified epidermal cells	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−

TABLE 2. Characters and character states. See Hickey (1973), Dilcher (1974), and text (pp. 30, 39) for more explanation.

1. Organization: Simple = S; Compound = C.
2. Base balance: Symmetrical = S; Asymmetrical = A.
3. Margin: Entire = E; Entire or crenate, but with glands = G; Toothed = T.
4. Venation: Brochidodromous = B; Weakly brochidodromous = W; Eucamptodromous = U.
5. Primary size: Moderate = m; Stout = S; Massive = M.
6. Secondary angle: Narrow (<45°) = N; Moderate = M; Wide (>65°) = W.
7. Angle of basal secondaries, relative to adjacent secondaries: More acute = A; Similar = S; More obtuse = O.
8. Angle of lower secondaries, relative to middle secondaries: More acute = A; Similar = S; More obtuse = O.
9. Angle of upper secondaries, relative to middle secondaries: More acute = A; Similar = S; More obtuse = O.
10. Secondary course: Curved uniformly = U; Curved abruptly = A.
11. Angle of secondary loops: Acute = A; Right = R; Obtuse = O.
12. Size of outer loops: Irregular = I; Uniform = U; Decreasing upwards = D; Absent = A.
13. Tertiary angle of origin, admedial: Acute = A; Right = R; Obtuse = O.
14. Tertiary angle of origin, exmedial: Acute = A; Right = R; Obtuse = O.
15. Tertiary pattern: Ramified = r; Random reticulate = R; Orthogonal reticulate = O; Weakly percurrent = W; Strongly percurrent, angle to midrib oblique = p; Strongly percurrent, angle to midrib predominantly right = P.
16. Simple intersecondaries: Absent = –; Present = +.
17. Composite intersecondaries: Absent = A; Infrequent (in fewer than 20% of intercostal areas) = I; Frequent (in more than 20% of intercostal areas) = F.
18. Intramarginal vein: Absent = –; Present = +.
19. Higher order vein pattern: Ramified = r; All random = R; 4° orthogonal, higher orders random = o; 4° and 5° orthogonal = O.
20. Higher order vein size: All moderate = M; 4° moderate, 5° fine = m; 4° and 5° fine = F; 4° moderate, 5° heavy = h.
21. Highest order present: 4° = 4; 5° = 5; 6° = 6.
22. Areole development: Incomplete = i; Imperfect = I; Well-developed = D.
23. Areole arrangement: Random = R; Ordered = O.
24. Areole shape: Irregular = I; Regular = R.
25. Areole size: Large = L; Medium = M; Small = S.

TABLE 2. Continued.

26. Veinlets: Absent = A; Simple = S; Branched 1–2× = 2; Branched 2–3× = 3.
27. Prismatic crystals in mesophyll: Absent = –; Present = +.
28. Prismatic crystals with veins: Absent = –; Present = +.
29. Druses in mesophyll: Absent = –; Present = +.
30. Druses with veins: Absent = –; Present = +.
31. Epidermal anticlinal walls, adaxial: Straight = S; Undulate = U.
32. Epidermal anticlinal walls, abaxial: Straight = S; Undulate = U.
33. Epidermal papillae: Absent = –; Present = +.
34. Stomatal location: Abaxial only = L; Primarily abaxial, but a few adaxial = b; Approximately equal on both surfaces = B.
35. Stomatal index (abaxial): <10% = A; 10–20% = B; >20% = C.
36. Stomatal type: Paracytic = P; Anisocytic = A.
37. Water stomata: Absent = –; Present = +.
38. Unicellular trichomes: Absent = A; Solitary = S; Some tufted = T.
39. Uniseriate, multicellular trichomes: Absent = –; Present = +.
40. Peltate trichomes: Absent = –; Present = +.
41. Filiform sclereids in mesophyll: Absent = –; Present = +.
42. Tanniniferous epidermal cells: Absent = –; Present = +.
43. Sclerified epidermal cells: Absent = –; Present = +.

Although technically marginal in position because no leaf tissue lies outside of it, this vein appears to be homologous to Hickey's (1973) intramarginal vein and I will use his term. See the description of *Bridelia* for more details.

26. Veinlets. The degree of branching of the freely-ending veinlets did not break down cleanly into simple, branched once, branched twice, etc. Instead, several degrees of branching were usually present within even a single leaf, although most veinlets branched within a limited range of degrees. The classes absent, simple (unbranched), branched 1–2 times, and branched 2–3 times appeared to reflect the variation more accurately.

35. Stomatal index. These classes appear to represent natural ranges that are distinct from each other in the Phyllanthoideae.

36. Stomatal type. Because both paracytic and brachyparacytic (Dilcher, 1974) stomata occur in many taxa, or even on the same leaf in many species in the Flueggeinae, I did not differentiate between these basically paracytic patterns in Tables 1 and 2. For the specific stomatal types, see the descriptions of the taxa.

37. Water stomata. Some *Andrachne* species bear large, apparently anomocytic stomata in addition to their more numerous, smaller anisocytic stomata (Fig. 54).

38. Unicellular trichomes. In the Phyllanthoideae, unicellular trichomes are usually simple with a peg-like, unmodified base and radial basal cells (Figs. 48, 57).

42. Tanniniferous epidermal cells. In several tribes, some of the epidermal cells are enlarged and spherical, with the adjacent cells forming a radial pattern (Figs. 58, 110). These contain tannins, according to Rothdauscher (1896) and Gaucher (1902); I have not attempted to confirm their reports.

43. Sclerified cells in the lower epidermis. See the descriptions of *Amanoa* and *Discocarpus* for more on these cells.

In addition to these characters, one character not among those listed in Table 2 but included in the descriptions below requires further explanation. Hickey (1971, 1977), based on his examination of cleared and fossil dicotyledon leaves, categorized the degree to which venation is organized into four levels or ranks. Rank is based primarily on the highest vein order in which the veins follow relatively regular courses and delimit areas of relatively consistent size and shape. If the secondary and higher order veins have irregular courses and the intercostal areas, therefore, are not uniform in size and shape, the organization is said to be first rank: only the primary vein has a regular course. If the secondary veins follow regular courses and the intercostal areas have uniform size and shape, but the tertiary and higher vein orders are disorganized, the level of organization is second rank. As the degree of organization increases further, the ranks increase to third and finally fourth, in which even the areoles show at least rudimentary orientation within domains. Leaves with low organizational rank appear first in the fossil record and, among living dicotyledons, the rank of foliar venation organization correlates well with the degree of advancement of the whole plant as determined by other evidence (Hickey, 1971, 1977; Hickey & Doyle, 1972; Doyle & Hickey, 1976).

In general, rank is fairly easy to assign by following Hickey's criteria. Problems may arise, however, with leaves from arid, arctic, or alpine habitats. In plants from these habitats, the organization of leaf venation frequently shows a regression below the level typical of their more temperate relatives, particularly in the lower vein orders (Hickey, 1977; Rury & Dickison, 1977). As a result, leaves can be found in which the higher order veins are more organized than are the lower order veins. It is not clear what ranks Hickey would assign in such cases. I recommend basing rank on the highest vein order that is regular in course, regardless of the behavior of lower order veins. In this way, the degree of evolutionary advancement achieved by the leaves will be better reflected by the rank assigned.

RESULTS

Table 1 summarizes the distribution of character states for the characters in Table 2. Two genera that I examined, *Poranthera* and *Reverchonia,* are not included in Table 1 because the extremely xeromorphic leaves of these genera contain too few characters.

In the discussion that follows I will first describe the leaf architecture and cuticular features of the subfamily. I will then describe each genus in turn, following the sequence in Webster's (1975) classification, including only those characters that are not adequately summarized in Tables 1 and 2. At the end of the generic descriptions for each tribe, I will discuss the taxonomic implications of the foliar morphology.

DESCRIPTIONS AND DISCUSSION

PHYLLANTHOIDEAE ASCHERSON

Leaves simple (compound in *Bischofia*), microphylls to mesophylls, some nanophylls; blades typically symmetrical, shape various; apex and base various; margin entire or crenate, toothed only in *Bischofia, Drypetes,* and *Putranjiva,* which bear theoid teeth; glands typically absent, if present then laminar or marginal; organization of venation typically second to third rank, but first or fourth rank in some; venation pinnate, brochidodromous to eucamptodromous, a few species kladodromous or reticulodromous; primary vein moderate to stout, rarely weak or massive, typically straight; secondary vein angle of divergence acute, uniform or varying, thickness moderate, curved uniformly or abruptly, loop-forming branches, if any, joining superadjacent secondary at acute to obtuse angle, only in *Bridelia* forming an intramarginal vein; intersecondary veins simple, composite, or absent; tertiary veins originating at various angles, reticulate or percurrent, in a few species ramified admedially, if percurrent straight or sinuous, branched or unbranched, oblique to primary vein with angle constant or decreasing upward or outward, typically alternate; higher order venation random to orthogonal, typically resolved to fifth or sixth order; marginal ultimate venation various; areoles imperfect to well developed, incomplete in some, arrangement random or oriented, shape typically irregular, size small to large; veinlets simple to branched three times, rarely absent; terminal tracheids normal or swollen; bundle sheath of primary vein almost always sclerified, higher order veins parenchymatous or sclerified; epidermal cells isodiametric, arrangement random or tetragonal to polygonal, anticlinal cell walls straight or undulate and typically unornamented, surface smooth or papillate; stomata typically only abaxial, on both surfaces in a few, orientation random, stomatal index about 8–25%, paracytic, brachyparacytic, parallelocytic, anisocytic, or, rarely, anomocytic, development mesogenous or mesoperigynous; trichomes typically unicellular with peg-like base and radial basal cells, some uniseriate with an unmodified base, rarely multiseriate or with a multicellular or enlarged head or branched; domatia absent except in *Bischofia* with marsupiform domatia; crystals typically present within leaf, single and prismatic or druses.

WIELANDIEAE BAILL. EX HURUSAWA

Wielandia Baill. (OTU 1)

W. elegans Baill., Seychelles: *Bernardi 14639* (BM). Figures 1, 2.

Leaves large microphylls, symmetrical, ovate-elliptic; apex acute; base acute; organization of venation high second rank; ultimate marginal venation incomplete, veins thickened and heavily sclerified, flaring toward the margin (Fig. 2); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Astrocasia Robn. & Millsp. (OTU 2)

A. neurocarpa (Muell. Arg.) I. M. Johnst., Mexico: Tamaulipas, *Stanford et al. 2264* (SUDH). Figures 3, 4, 7.

A. peltata Standl., Mexico: Tres Marias Island, *Howell 10405* (CAS).

A. phyllanthoides Robn. & Millsp., Mexico: Yucatan, *Gaumer 475* (UC).

Leaves microphylls to small mesophylls, symmetrical, very wide ovate to orbiculate; apex rounded or emarginate; base rounded or peltate; organization of venation mid third rank; marginal ultimate venation fimbriate; terminal tracheids normal (*A. peltata, A. phyllanthoides*) or swollen (*A. neurocarpa*); bundle sheath parenchymatous (*A. phyllanthoides*) or sclerified (*A. neurocarpa, A. peltata*); stomata brachyparacytic; lower epidermis papillate (*A. phyllanthoides*) or smooth.

Blotia Leandri (OTU 9)

B. oblongifolia (Baill.) Leandri, Madagascar: *Serv. For. 6157* (P). Figures 5, 6.

Leaves mesophylls, symmetrical, narrow elliptic; apex acuminate; base obtuse; organization of venation low third rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic.

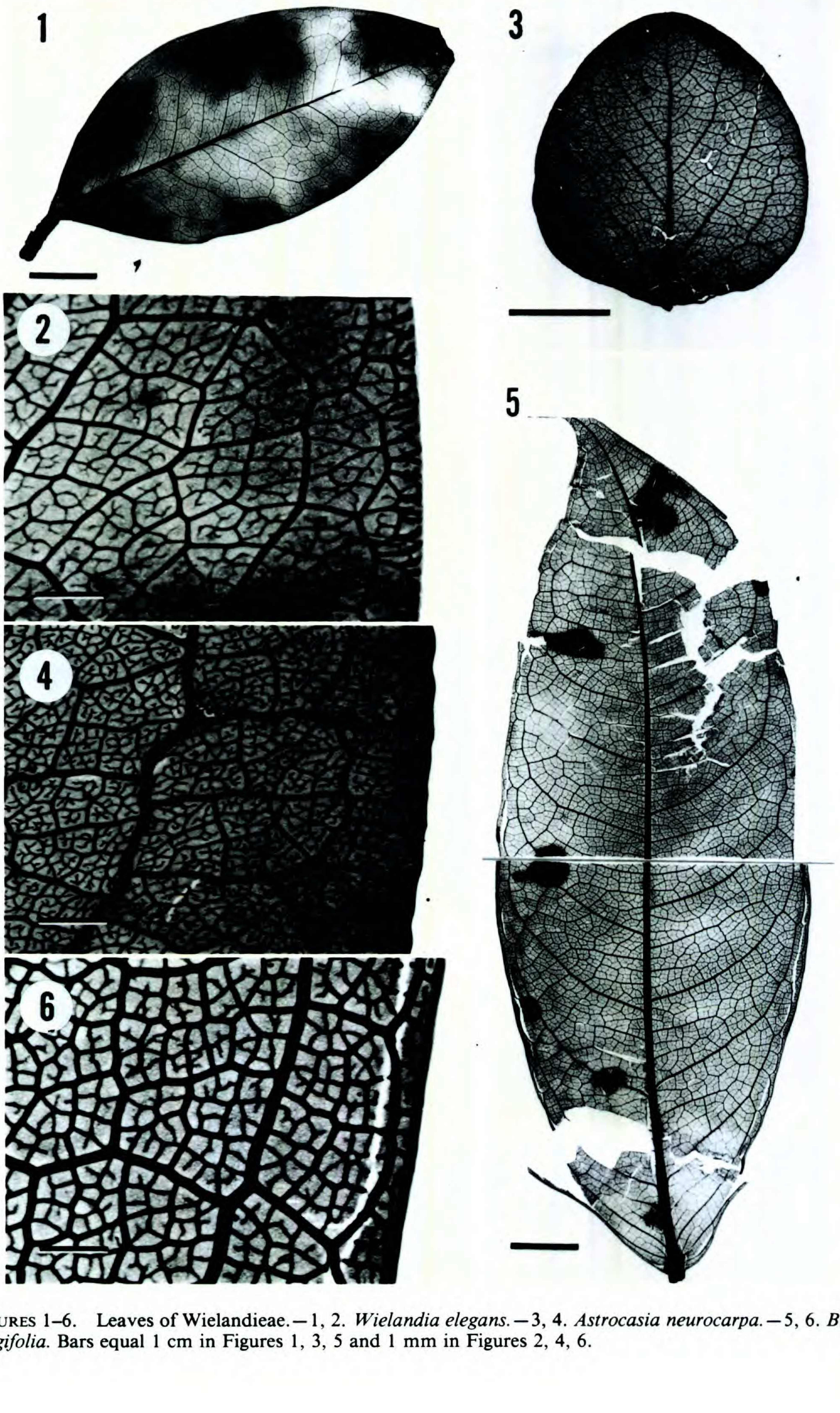
Discocarpus Klotzsch (OTU 5)

D. spruceanus Benth., Guiana: *Spruce 3527* (MO). Figures 8, 9.

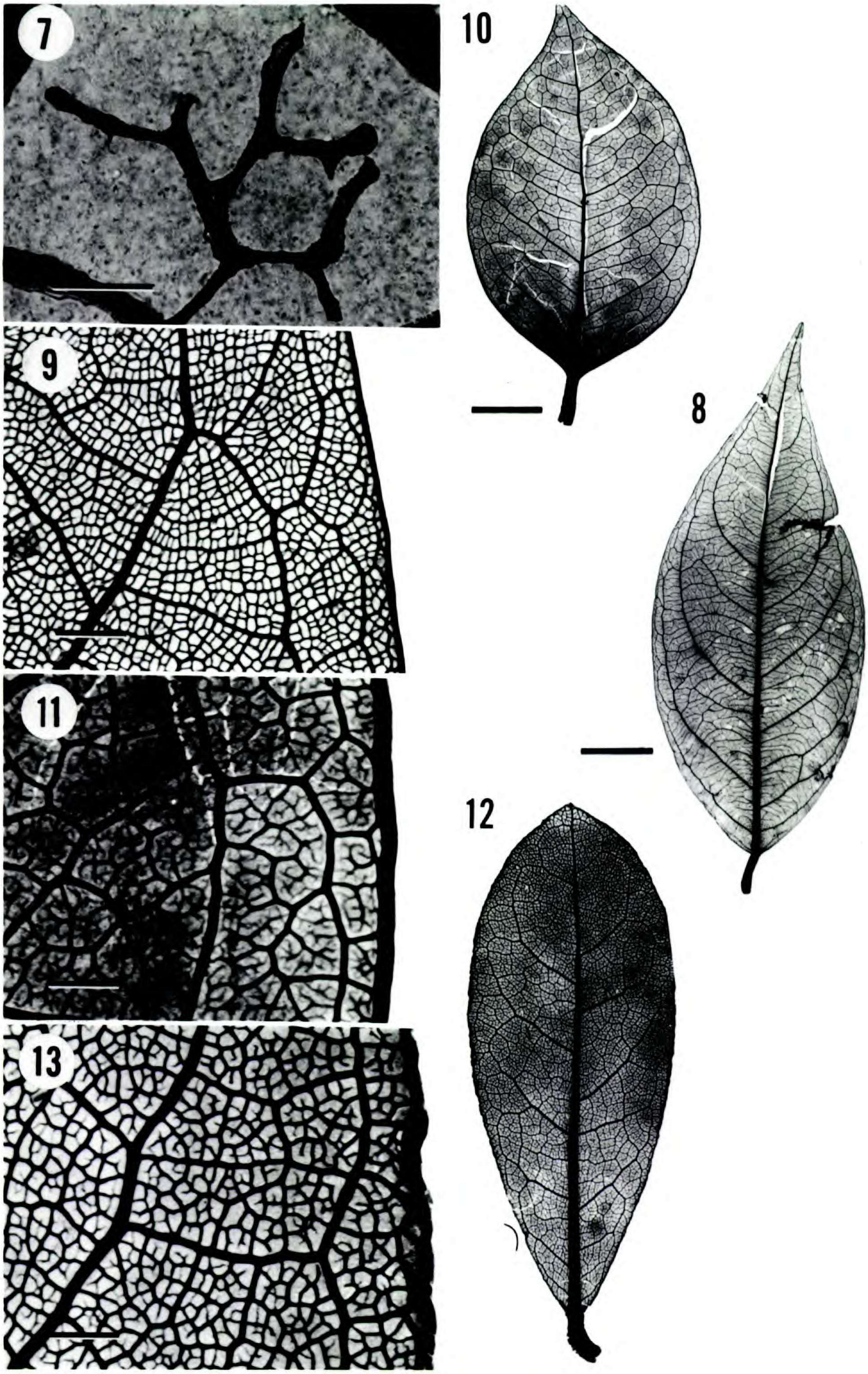
Leaves microphylls, symmetrical, elliptic; apex attenuate; base obtuse; organization of venation mid fourth rank (but see below); marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous, but extensions sclerenchymatous; stomata brachyparacytic.

My anatomical observations agree with descriptions by Rothdauscher (1896) and Gaucher (1902).

The leaves of *Discocarpus* are remarkable in many respects. Although the higher order venation is strikingly orthogonal, forming extremely well developed areoles, the lower order venation is much less organized, with uncommon simple intersecondaries and weakly percurrent tertiaries that are quite irregular and sinuous in course. Freely-ending veinlets are rare, and when present are simple and straight. This pattern appears to be the result of a trend, involving several genera, of decreasing organization of lower order venation and increasing organization of higher order venation. Stomatal frequency is very high, with most cells in the lower epidermis appearing to be subsidiary cells



FIGURES 1–6. Leaves of Wielandieae.—1, 2. *Wielandia elegans.*—3, 4. *Astrocasia neurocarpa.*—5, 6. *Blotia oblongifolia.* Bars equal 1 cm in Figures 1, 3, 5 and 1 mm in Figures 2, 4, 6.



FIGURES 7–13. Leaves of Wielandieae.—7. *Astrocasia neurocarpa,* swollen terminal tracheids.—8, 9. *Discocarpus spruceanus.*—10, 11. *Heywoodia lucens.*—12, 13. *Lachnostylis hirta.* Bars equal 1 cm in Figures 8, 10, 12; 1 mm in Figures 9, 11, 13; and 100 μm in Figure 7.

or guard cells. The lower epidermis is also strongly sclerified, with the outer wall of most cells thickened (cf. *Amanoa,* below).

Heywoodia Sim. (OTU 3)
H. lucens Sim., Tanganyika: *Watkins 453* (EAH). Figures 10, 11.

Leaves microphylls, symmetrical, elliptic; apex acuminate; base obtuse-cuneate; tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Lachnostylis Turcz. (OTU 4)
L. hirta (L. f.) Muell. Arg., South Africa: *Burchell 5213* (G). Figures 12, 13.

Leaves microphylls, symmetrical, oblanceolate; apex obtuse; base acute; organization of venation high second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata brachyparacytic, rarely each subsidiary cell divided again by a wall perpendicular to the guard cells.

My anatomical observations agree with the reports of Rothdauscher (1896) and Gaucher (1902).

Pentabrachium Muell. Arg. (OTU 13)
P. reticulatum Muell. Arg., Cameroons: *Zenker 3869* (MO). Figures 14, 15.

Leaves mesophylls, symmetrical, ovate-elliptic; apex long acuminate; base obtuse; organization of venation mid third rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

Petalodiscus Baill. (OTU 8)
P. danguyana Leandri, Madagascar: *Schlieben 8120* (UC). Figures 16, 17.

Leaves microphylls, symmetrical, narrow ovate-elliptic; apex acuminate; base obtuse; organization of venation low fourth rank (but see below); marginal ultimate venation incomplete to weakly looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic.

The leaves of *Petalodiscus,* as do those of *Discocarpus,* exhibit an unusual combination of relatively disorganized lower order venation with highly differentiated orthogonal higher order venation forming oriented, but still imperfect areoles.

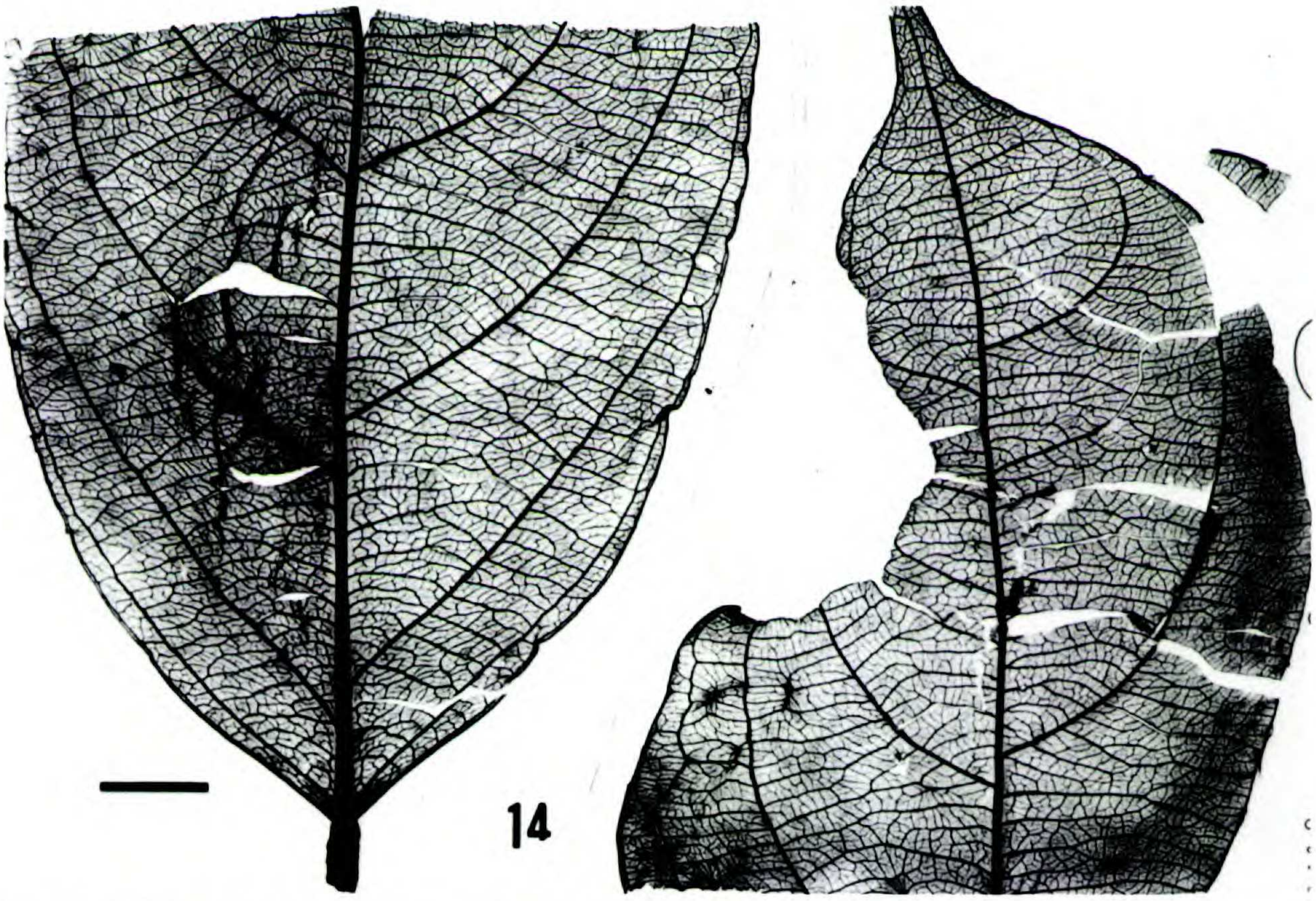
Savia Willd.
Sect. *Heterosavia* Urb. (OTU 6)
- *S. bahamensis* Britt., U.S.A.: Florida, *Caldwell 8782* (UC). Figures 18, 19, 22.
- *S. clementis* Alain, Cuba: *Clemente et al. 4036* (DAV).
- *S. clusiifolia* Griseb., Cuba: *Alain & Clemente 1485* (DAV).
- *S. cuneifolia* Urb., Cuba: *Alain & Clemente 919* (DAV).
- *S. erythroxyloides* Griseb., Haiti: *Leonard 8334* (UC).

Sect. *Savia* (OTU 7)
- *S. sessiliflora* Willd., Haiti: *Holdridge 1415* (UC). Figures 20, 21.

Leaves microphylls, symmetrical, obovate or elliptic; apex acute, obtuse, rounded, or emarginate; base acute-decurrent or cuneate or obtuse; organization of venation low to mid third rank; marginal ultimate venation looped or fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or lightly sclerified; stomata paracytic or occasionally parallelocytic (Fig. 22).

My observations agree with earlier reports on *S. bahamensis, S. clusiifolia, S. erythroxyloides,* and *S. sessiliflora* (Rothdauscher, 1896; Gaucher, 1902; Hayden, 1980).

The leaves of the genera Webster placed in the Wielandieae generally form a homogeneous group. Two genera appear anomalous; however. *Astrocasia,* with its weakly percurrent tertiaries and narrow intercostal areas, appears more similar to some members of the Phyllantheae, a relationship suggested by both Punt (1962) and Köhler (1965) on the basis of pollen and even by Webster in an earlier paper (Webster, 1956). The leaves of *Pentrabrachium* are also of higher rank than typical of the Wielandieae, and further differ in the eucamptodromous secondaries, the presence of unicellular trichomes, and the undulate anticlinal walls of the epidermal cells. In these and other characters, *Pentabrachium* is much like *Dicoelia,* with which it shares the unusual condition of having the lower and medial secondaries eucamptodromous and the apical secondaries brochidodromous. Both phenetic and cladistic analyses of leaf characters suggest a close relationship between these genera (Levin, 1986 and in press), a possibility that has not been pro-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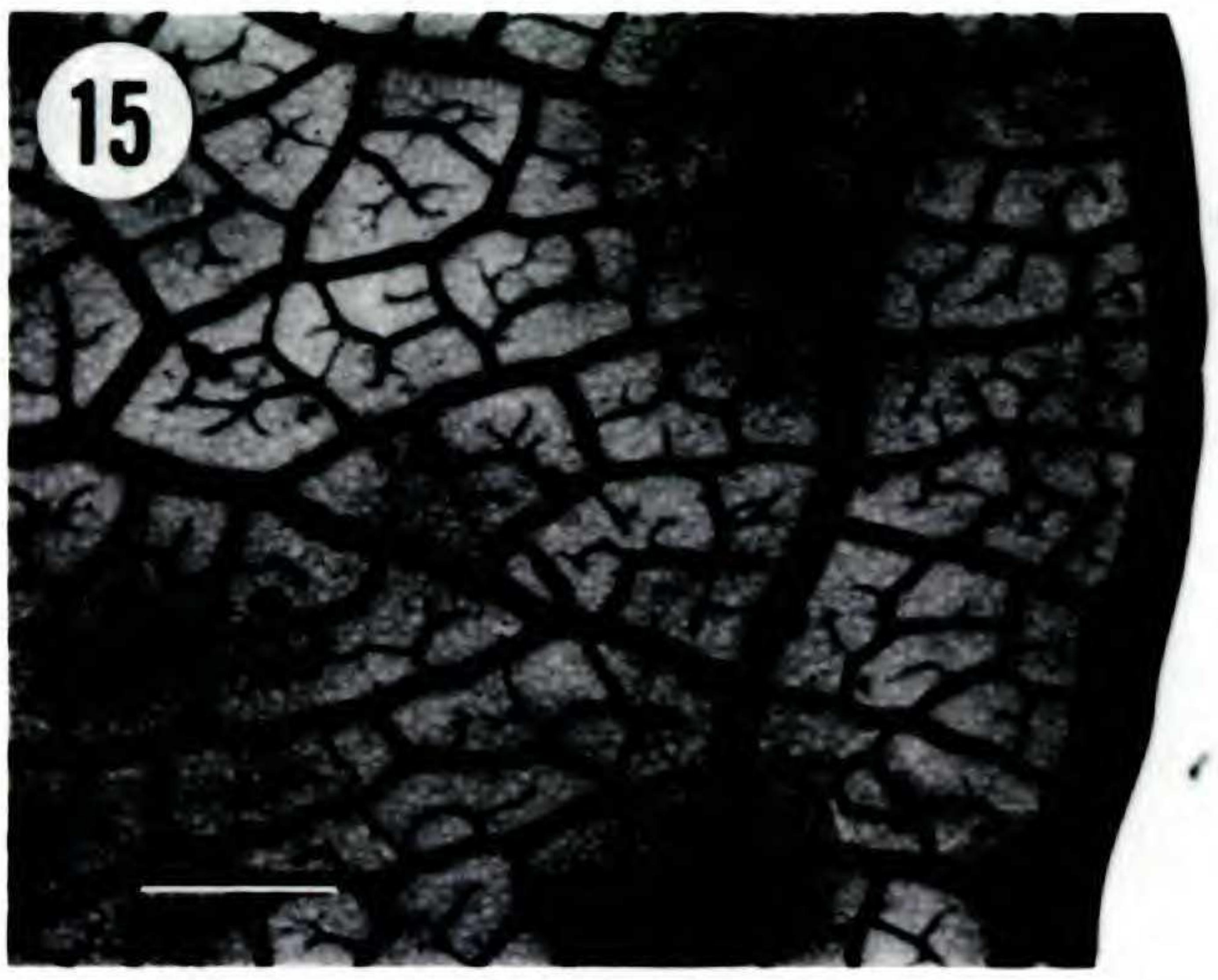
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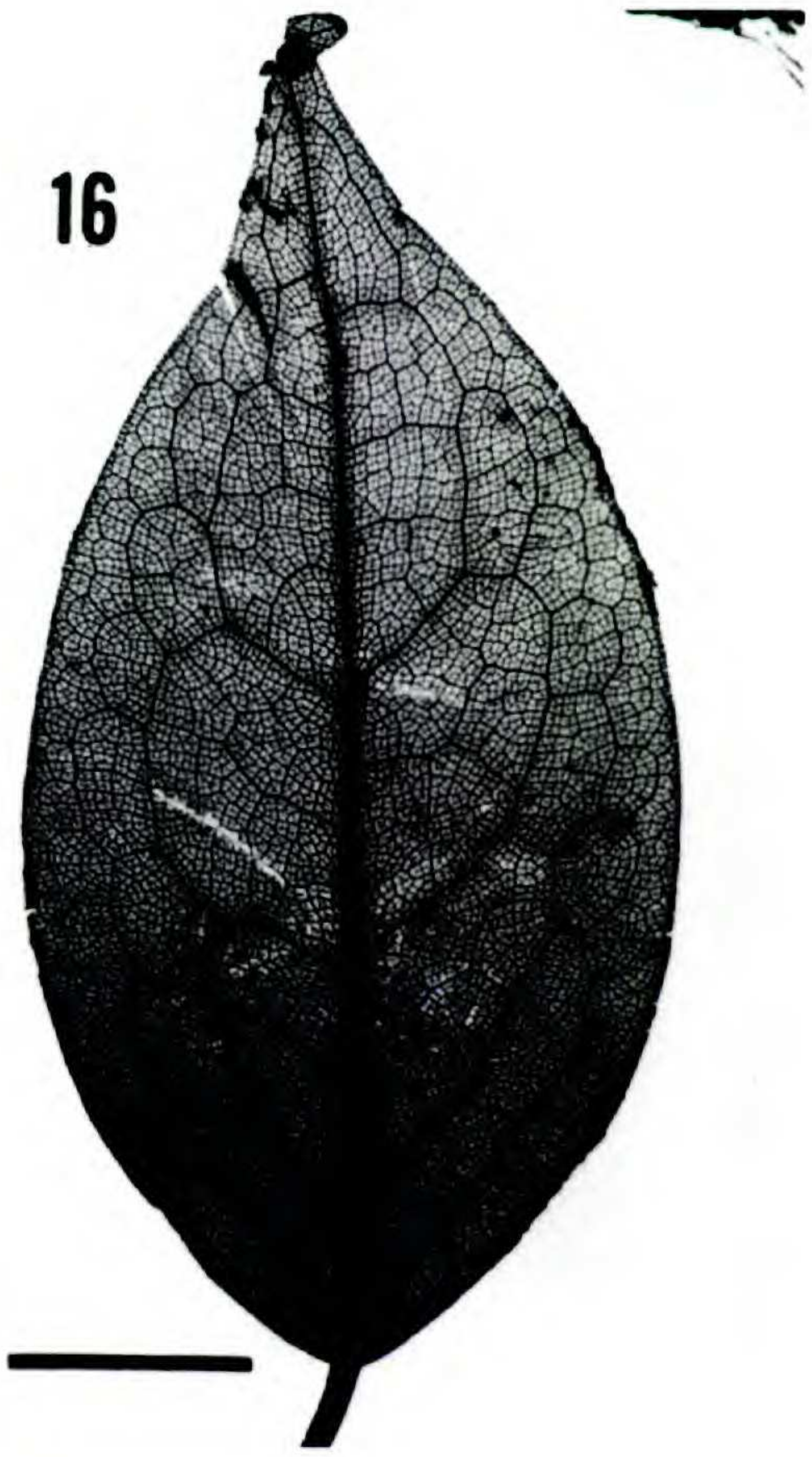
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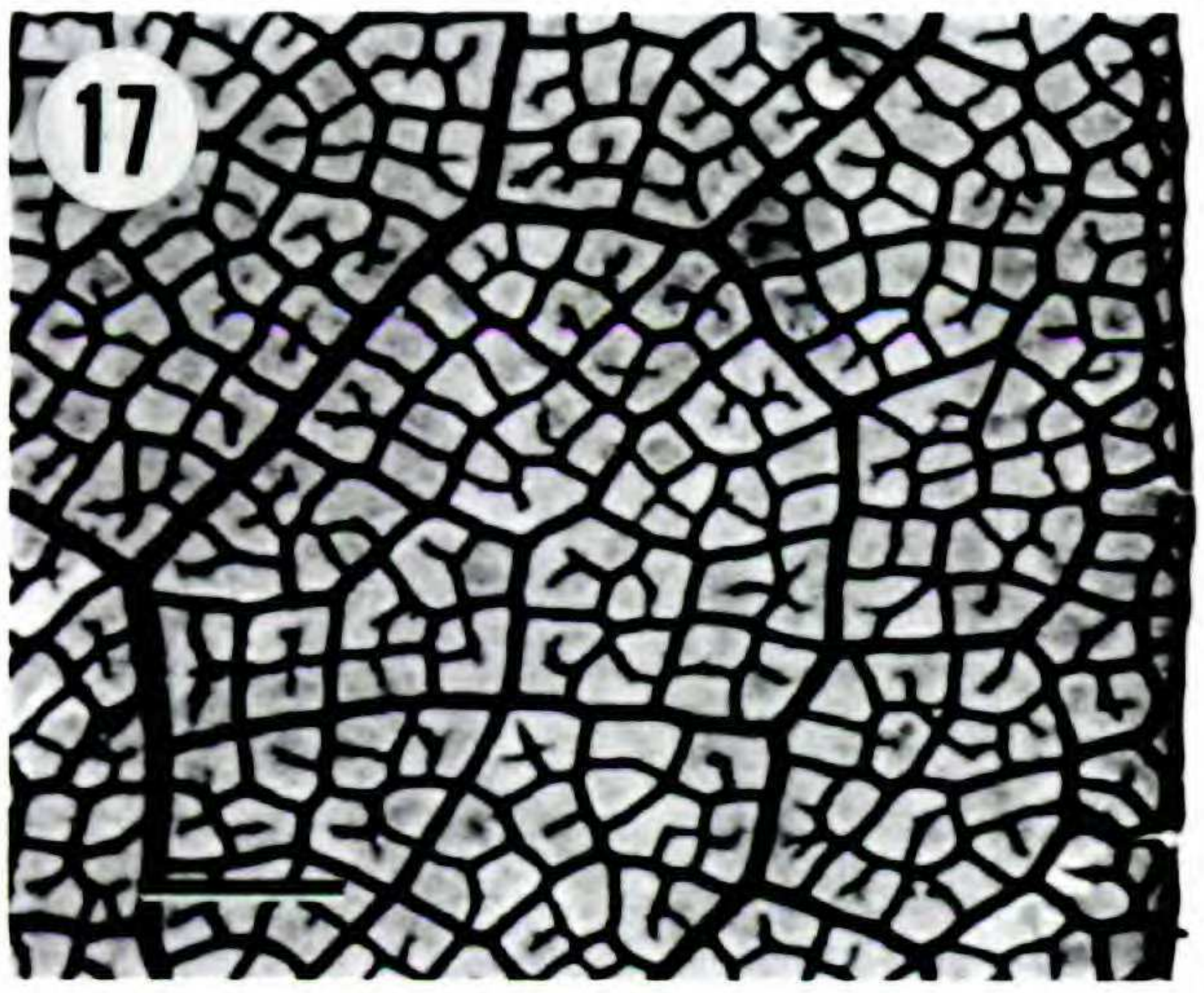
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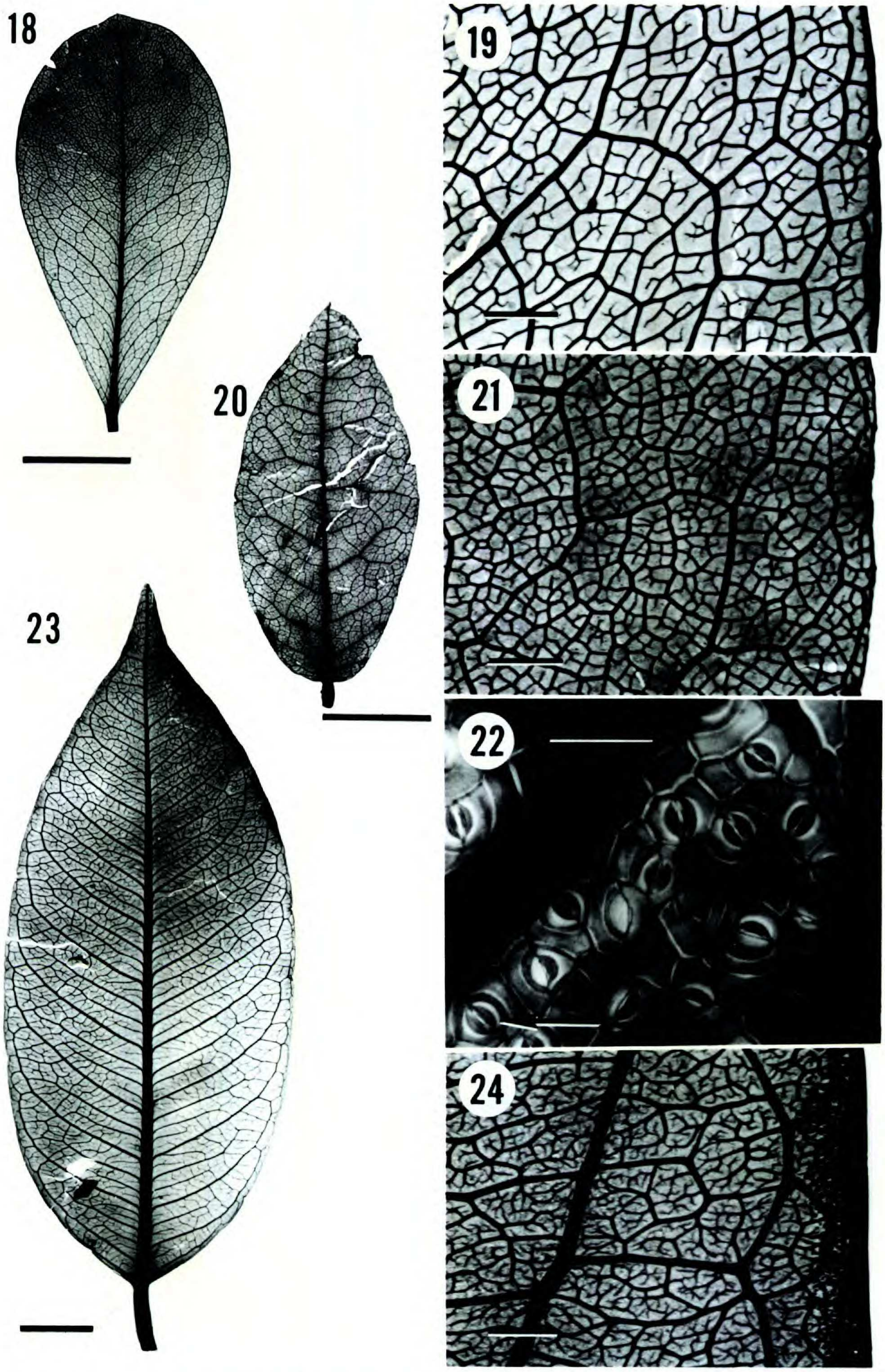
FIGURES 14–17. Leaves of *Pentabrachium* and *Petalodiscus*.—14, 15. *Pentabrachium reticulatum*.—16, 17. *Petalodiscus danguyana*. Bars equal 1 cm in Figures 14, 16 and 1 mm in Figures 15, 17.



FIGURES 18–24. Leaves of *Savia* and *Amanoa*.—18, 19. *Savia bahamensis*.—20, 21. *S. sessiliflora*.—22. *S. bahamensis*, abaxial epidermis, showing paracytic and parallelocytic (arrow) stomata.—23. *Amanoa oblongifolia*.—24. *A. guianensis*. Darkening of margin is due to sclerified epidermal cells. Bars equal 1 cm in Figures 18, 20, 23; 1 mm in Figures 19, 21, 24; and 50 μm in Figure 22.

TABLE 3. Epidermal characters in species of *Amanoa.*

	Cell Size Patterns		Sclerified Cells	
Species	Adaxial	Abaxial	Adaxial	Abaxial
glaucophylla	small cells in groups of 5–15 with matrix of large cells	small and large cells randomly mixed	dense near margin	scattered isolated cells and small groups of cells in intercostal areas; dense beneath low order veins and near margin
grandifolia	small and large cells randomly mixed	small and large cells randomly mixed	none or scattered near margin	scattered isolated cells and small groups of cells in intercostal areas; dense beneath low order veins and near margin
guianensis	small and large cells randomly mixed	two size classes not well differentiated	none or scattered near margin	few scattered isolated cells in intercostal areas; dense beneath low order veins and near margin
oblongifolia	only small cells present	only small cells present	scattered isolated cells in intercostal areas; dense over low order veins and near margin	almost all cells sclerified, except scattered groups in intercostal areas and stomatal cells

posed previously but that deserves further consideration.

Blotia, Petalodiscus, Savia, and *Discocarpus* appear to form a closely related group. A trend toward disorganization of the lower order venation coupled with increasing organization of the higher order venation, a very unusual pattern, can be traced from *Savia* sect. *Heterosavia* through sect. *Savia* to *Petalodiscus* and *Discocarpus. Blotia* is quite similar to *Savia,* differing mainly in the large size of its leaves.

AMANOEAE (PAX & HOFFM.) WEBST.

Amanoa Aubl. (OTU 10)

A. glaucophylla Muell. Arg., Guyana: Amazonas, *Krukoff 6370* (A). Figure 25.

A. grandifolia Muell. Arg., Venezuela: *Pittier 14799* (UC). Figures 26–28.

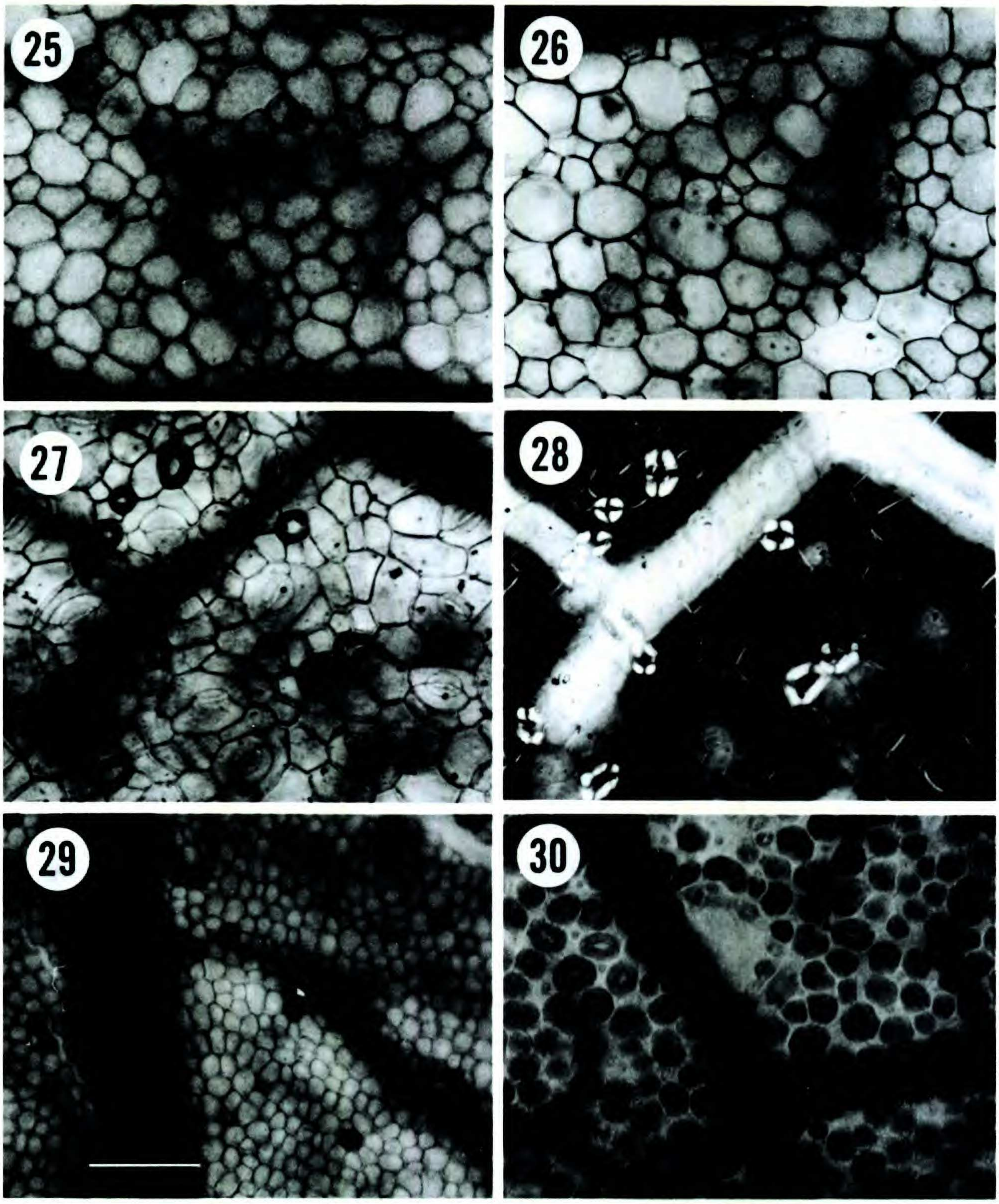
A. guianensis Aubl., Venezuela: *Cardona 401* (UC). Figure 24.

A. oblongifolia Muell. Art., Guyana: Amazonas, *Krukoff 7015* (A). Figures 23, 29, 30.

Leaves microphylls to mesophylls, symmetrical, oblong or elliptic; apex acuminate; base acute, obtuse, or rounded; organization of venation low third rank; marginal ultimate venation looped or weakly fimbriate; terminal tracheids normal to slightly enlarged; bundle sheath of higher order veins parenchymatous; stomata paracytic or rarely parallelocytic.

Of the seven to nine species in this genus, the leaves of only *A. glaucophylla* and *A. oblongifolia* have previously been described (Rothdauscher, 1896; Gaucher, 1902; Hayden, 1980). My observations agree with the earlier descriptions except for Rothdauscher's report, repeated by Metcalfe and Chalk (1950), of papillae and corkworts in the lower epidermis of *A. glaucophylla.* Reports of enlarged terminal tracheids vary in the literature. My observations suggest that this is a variable character within the genus, perhaps even within some of the species.

As observed by Rothdauscher, Gaucher, and Hayden, cells of the lower epidermis of *Amanoa* exhibit different patterns of sclerification. In addition, rather than being of relatively uniform size as in most phyllanthoids, the epidermal cells of most *Amanoa* species are of two sizes: larger cells with diameters of about 35 μm and smaller cells with diameters of about 16 μm. The distributions of cells of the two sizes vary from species to species. Table 3 details the distribution of large and small cells and sclerified cells in the four species I examined; some of the patterns are illustrated in Figures 25–30. The variation in these

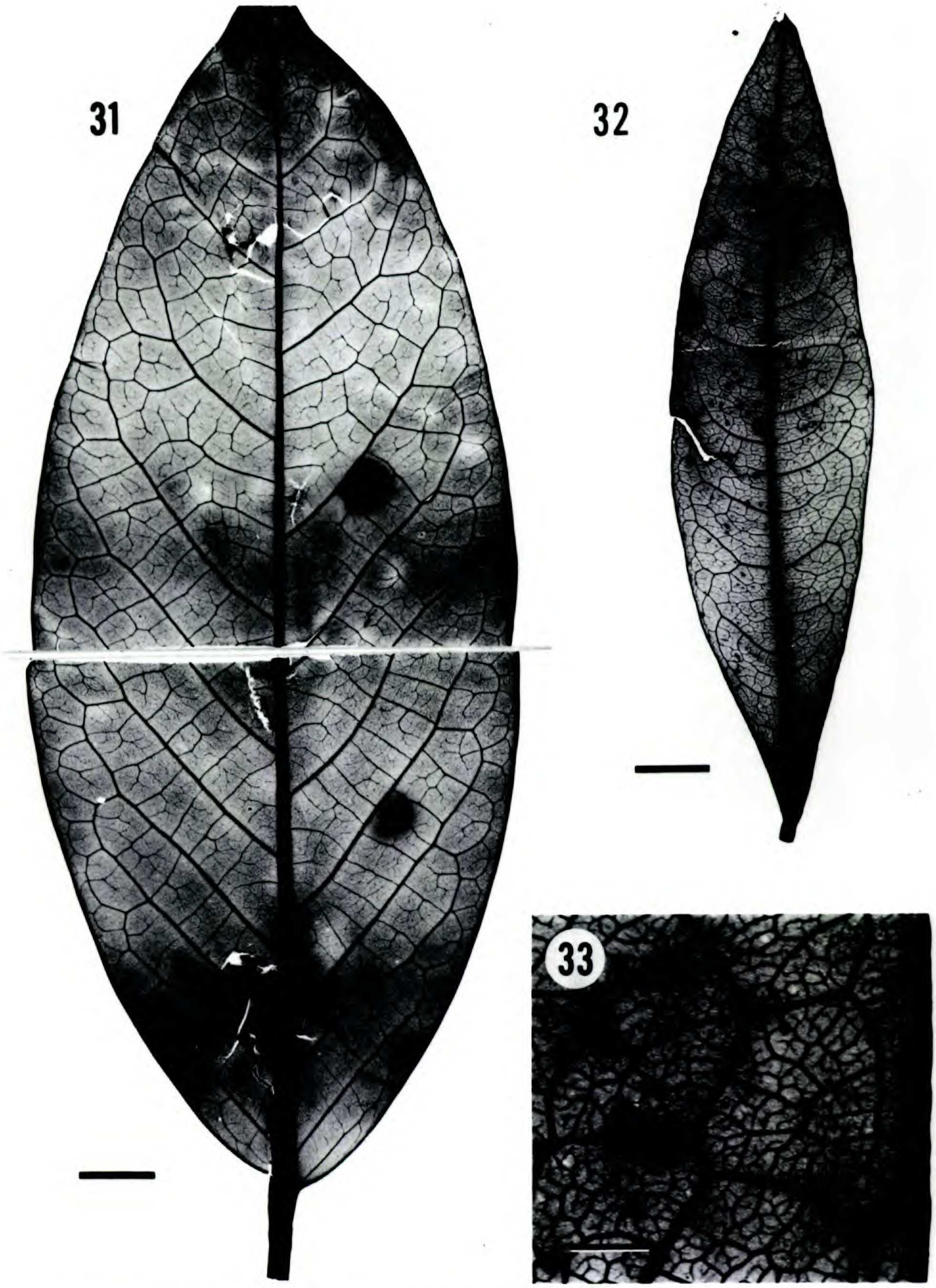


FIGURES 25–30. Epidermal cell patterns of *Amanoa.* Compare with Table 3.—25. *A. glaucophylla,* adaxial epidermis.—26. *A. grandifolia,* adaxial epidermis.—27, 28. *A. grandifolia,* abaxial epidermis, photographed with normal and polarized light, respectively. Sclerified cells are bright with polarized light.—29, 30. *A. oblongifolia,* adaxial and abaxial epidermis respectively. Bar equals 100 μm.

epidermal characters in the different species and the apparent constancy of the patterns within species suggest that the patterns may be useful in classification and identification.

Actephila B1.
Group 1 (OTU 11)
A. anthelminthica Gagnep., Annam: *Poilane 9216* (UC).
A. nitidula Gagnep., Cochinchina: *Pierre (1907)* (UC). Figures 32, 33.

Leaves microphylls, symmetrical, narrow elliptic; apex acute; base acute-cuneate; organization of venation mid second rank; marginal ultimate venation incomplete (*A. anthelminthica*) or fimbriate (*A. nitidula*); terminal tracheids normal or slightly swollen; bundle sheath of higher order veins parenchymatous; stomata paracytic.



FIGURES 31–33. Leaves of *Actephila*.—31. *A. excelsa*.—32, 33. *A. nitidula*. Bars equal 1 cm in Figures 31, 32 and 1 mm in Figure 33.

Group 2 (OTU 12)
A. excelsa (Datz) Muell. Arg., Philippines: Mindanao, *Ramos & Edano 49158* (UC). Figure 31.

Leaves mesophylls, symmetrical, narrow ovate; apex acuminate; base rounded; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

As Table 2 and the descriptions indicate, the leaves of *Actephila* form a very heterogeneous group. Comparison with uncleared leaves of these and other species indicated that this variation is not an artifact of my small sample size; assessing the taxonomic significance of this variation requires study of cleared leaves from more species.

Croizatia Steyerm. (OTU 93)
C. naiguatensis Steyerm., Venezuela: *Tillett et al. 82* (DAV). Figures 34, 35.

Leaves mesophylls, symmetrical, elliptic; apex acute; base acute-decurrent; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis and beneath midrib.

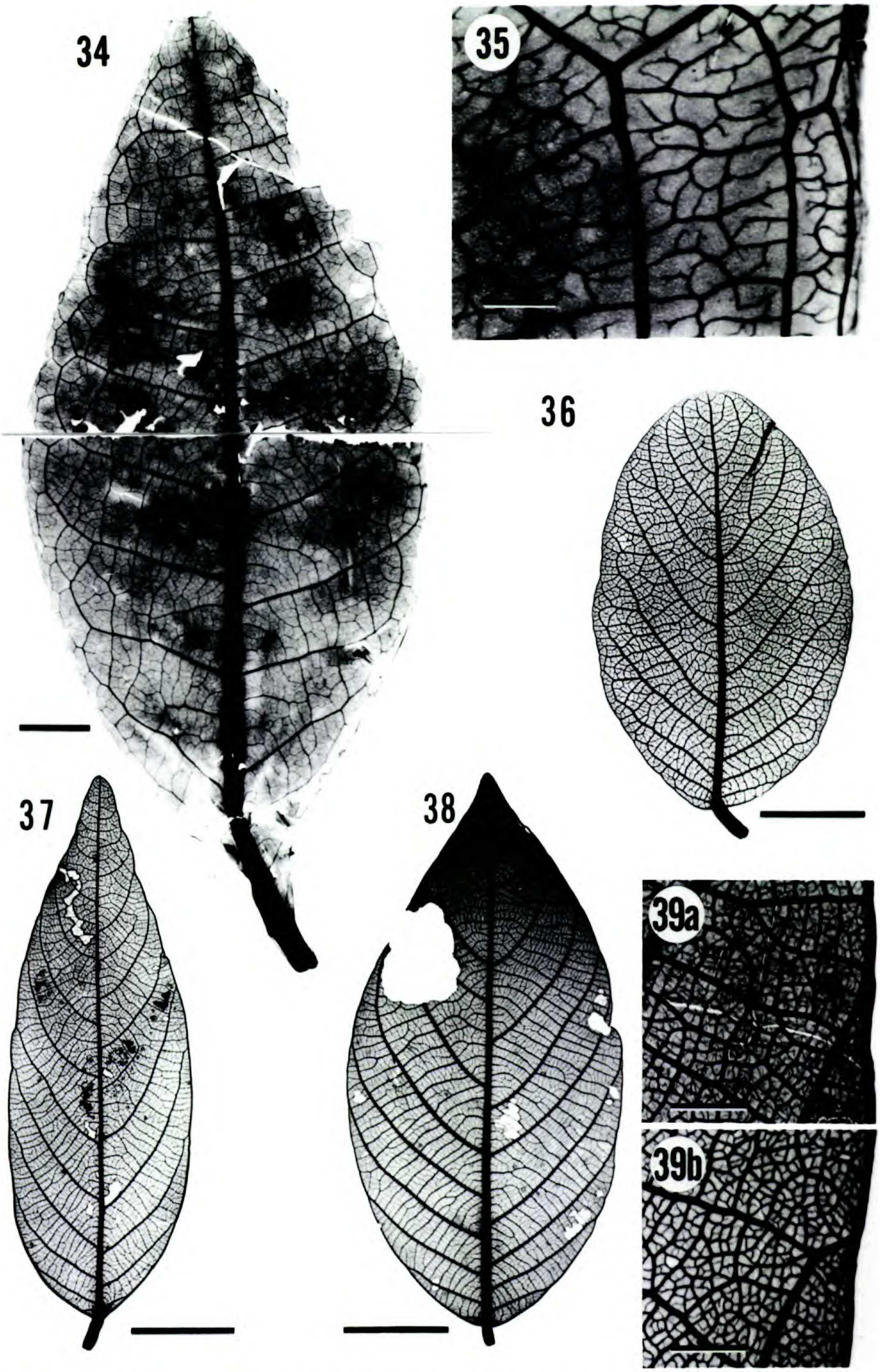
Although *Actephila* and *Amanoa* have traditionally been placed together, pollen of the two genera appears to be quite different (Punt, 1962; Köhler, 1965), as does the wood (Metcalfe & Chalk, 1950; Hayden, 1980). Leaf morphology does little to resolve the controversey. Cladistic and phenetic analyses of leaf characters place *Amanoa* near the Wielandieae, particularly *Wielandia, Blotia,* and *Savia* sect. *Heterosavia,* a position implied by Webster's classification and suggested by pollen and wood anatomy (Levin, 1986 and in press). The position of *Actephila* is less clear, largely due to the heterogeneity of its leaves. Leaves of *Actephila anthelminthica* and *A. nitidula* suggest a fairly close relationship to *Amanoa* and the Wielandieae, whereas the leaves of *A. excelsa* share more with the leaves of *Andrachne,* a relationship first proposed by Baillon (1858) and later supported by both Punt (1962) and Köhler (1965) on the basis of pollen. A relationship between *Actephila* and *Andrachne* is also more consistent with wood anatomy than is the association of *Actephila* and *Amanoa* (Metcalfe & Chalk, 1950; Hayden, 1980). Further study of leaves and other organs of *Actephila* will be necessary to clarify the relationships of this genus.

When Steyermark (1952) described *Croizatia,* he allied it with *Actephila* on the basis of strikingly similar fruits. Leaf morphology suggests a closer relationship to *Savia* and its relatives, particularly *Blotia.* More sampling within *Actephila* could conceivably turn up species more similar to *Croizatia* than the three I examined. Because male flowers of *Croizatia* remain unknown, the pollen has never been examined. We are similarly ignorant of most other aspects of the biology of this little known genus.

BRIDELIEAE MUELL. ARG.

Bridelia Willd.
Group 1 (OTU 14)
  Sect. *Micranthae* Gehrm.
    B. atroviridis Muell. Arg., Cameroons: *Breteler 2866* (UC).
  Sect. *Scleroneurae* Gehrm.
    B. cathartica Bertol. f., Tanganyika: *Tanner 3541* (UC).
    B. exaltata F. v. M., Australia: Queensland, *Kajewski 72* (UC). Figure 36.
    B. mollis Hutch., Rhodesia: *Wormald (1951)* (UC).
Group 2 (OTU 15)
  Sect. *Cleistanthoideae* Gehrm.
    B. balansae Tutch., China: Kwangtung, *Chun 5982* (UC).
    B. glauca Bl., Sumatra: *Boeea 7657* (UC). Figure 40.
    B. minutiflora Hook. f., Philippines: *Ramos (1925)* (UC).
Group 3 (OTU 16)
  Sect. *Micranthae* Gehrm.
    B. glabrifolia (Muell. Arg.) Merr., Philippines: *Ramos & Edano (1924)* (UC). Figure 37.
    B. micrantha (Hochst.) Baill., Ivory Coast: *de Wilde 452* (UC). Figure 39b.
  Sect. *Scleroneurae* Gehrm.
    B. monoica (Lour.) Merr., Sumatra: *Boeea 8440* (UC). Figures 38, 39a.
    B. scleroneura Muell. Arg., Tanganyika: *Tanner 4160* (UC).
  Sect. *Stipulares* Gehrm.
    B. stipularis (L.) Bl., Sumatra: *Boeea 8275* (UC).

Leaves microphylls or mesophylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate; organization of venation high third rank; marginal ultimate venation fimbriate or consisting of an intramarginal vein formed by the stiffening of the brochidodromous loops (see below); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic, rarely one of the subsidiary cells divided by an additional wall perpendicular to the guard cells; trichomes typically at least beneath low order veins, may also



FIGURES 34–39. Leaves of *Croizatia* and *Bridelia*.—34, 35. *Croizatia naiguatensis*.—36. *Bridelia exaltata*.—37. *B. glabrifolia*.—38, 39a. *B. monoica*.—39b. *B. micrantha*. Bars equal 1 cm in Figures 34, 36–38 and 1 mm in Figures 35, 39a, b.

be scattered on abaxial or less commonly adaxial surfaces, rarely the leaves glabrous.

Gaucher (1902) reported sclerified bundle sheaths in *B. micrantha, B. obtusa,* and *B. zenkeri.*

Although all the species of *Bridelia* I examined are identified easily by their numerous secondaries and closely spaced, regularly and strongly percurrent tertiaries, three groups of species can be recognized on the basis of the patterns formed by the outer portion of the secondaries and the marginal ultimate venation. The first group, which includes some members of sects. *Micranthae* and *Scleroneurae,* has weakly brochidodromous secondaries and fimbriate marginal ultimate venation (Fig. 36). The second group, all members of sect. *Cleistanthoideae,* also has a fimbrial vein, but the secondaries are eucamptodromous (Fig. 40). In the third group, the secondary veins are brochidodromous with the outer portions of the loops forming an intramarginal vein. Close examination reveals that in some species, members of sects. *Stipulares* and *Scleroneurae,* the loops join without any abrupt change of direction (Figs. 38, 39a), whereas in other species, members of sect. *Micranthae,* each secondary vein bends sharply exmedially within 1 mm or less of joining the intramarginal vein (Figs. 37, 39b). As both *Micranthae* and *Scleroneurae* also contain species with the first leaf type, this difference may reflect independent origin of the intramarginal vein in the two sections. Resolving this and the question of the relationship of the eucamptodromous *Cleistanthoideae* awaits study of more species in this genus of over 60 species.

Cleistanthus Hook. f. ex Planch.
Group 1 (OTU 17)
- *C. acuminatissimus* Merr., British N Borneo: *Elmer 21153* (UC). Figures 41, 42.

Group 2 (OTU 18)
- Sect. *Stipulati* Jabl.
  - *C. bridelifolius* C. B. Rob., Sarawak: *Chew Wee-Lek 558* (UC).
  - *C. siamensis* Craib, Annam: *Poilane 5186* (UC).

Group 3 (OTU 19)
- Sect. *Ferruginosi* Jabl.
  - *C. barrosii* Merr., Philippines: *Clemens 16870* (UC). Figure 43.
  - *C. ferrugineus* Muell. Arg., Ceylon: *Galston 2233* (UC).
- Sect. *Pedicellati* Jabl.
  - *C. integer* C. B. Rob., Philippines: *Loger 12372* (UC), *Ramos & Edano (1926)* (UC).

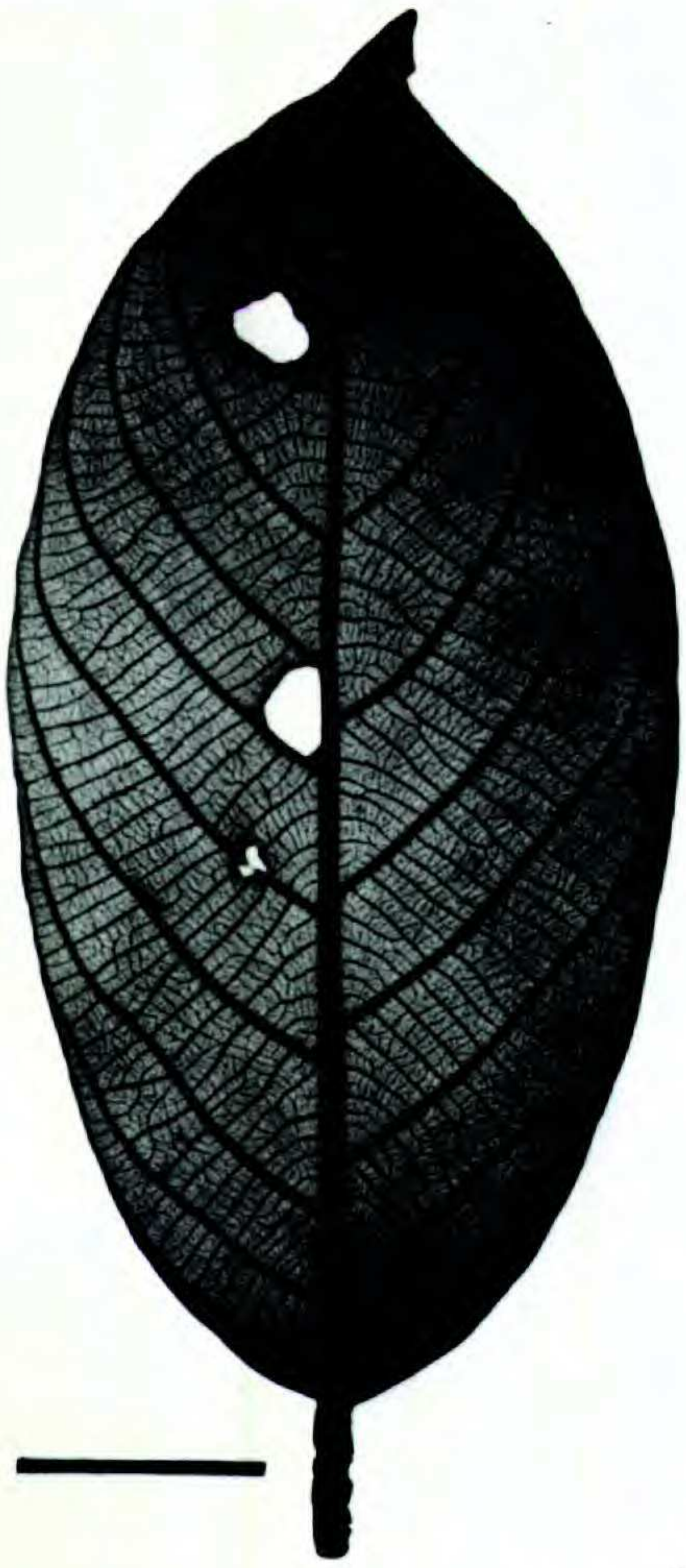


FIGURE 40. Leaf of *Bridelia glauca.* Bar equals 1 cm.

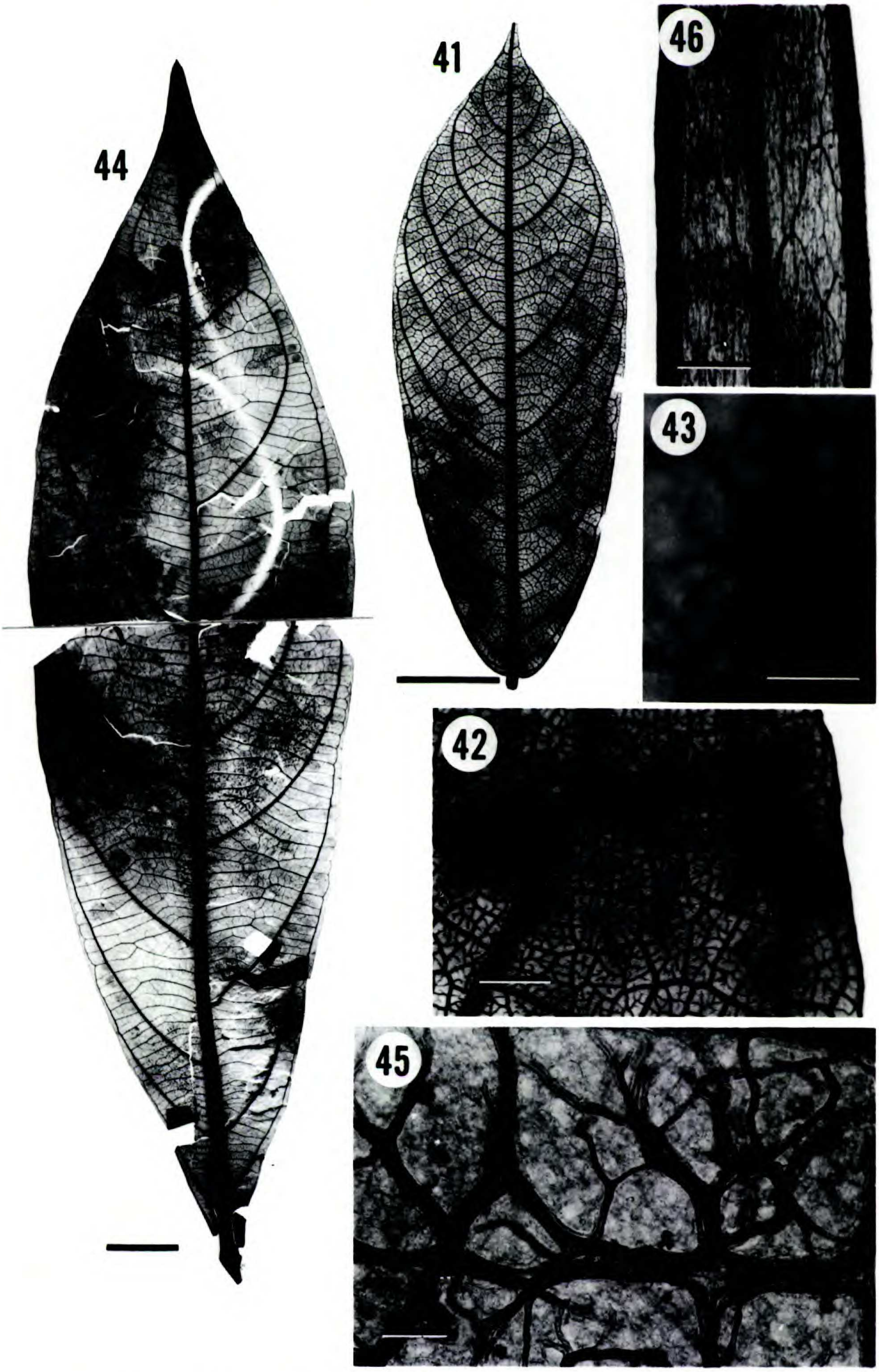
Group 4 (OTU 20)
- Sect. *Chartacei* Jabl.
  - *C. cunninghamii* Muell. Arg., Australia: Queensland, *Clemens (1944)* (UC).

Group 5 (OTU 21)
- Sect. *Cleistanthus*
  - *C. polystachyus* Hook. f. ex Planch., Ivory Coast: *Leeuwenberg 3736* (UC).

Group 6 (OTU 22)
- *C. saichikii* Merr., China: Hainan, *Lau 15* (UC).

Group 7 (OTU 23)
- Sect. *Australes* Jabl.
  - *C. micranthus* Croizat, Fiji: *Smith 9531* (UC).

Group 8 (OTU 24)
- Sect. *Leiopyxis* (Miq.) Jabl.
  - *C. apodus* Bth., Australia: Queensland, *Irvine 670* (DAV).
  - *C. blancoi* Rolfe, Philippines: *Ramos & Edano* 1928 (UC).



FIGURES 41–46. Leaves of *Cleistanthus, Dicoelia,* and *Poranthera.*—41, 42. *Cleistanthus acuminatissimus.*—43. Dolabrate trichome of *C. barrosii.*—44. *Dicoelia affinis.*—45. Filiform sclereids of *D. affinis.*—46. *Poranthera corymbosa.* Bars equal 1 cm in Figures 41, 44; 1 mm in Figures 42, 46; and 100 μm in Figures 43, 45.

C. ripicolus Leonard, Nigeria: *Onochie FHI 33213* (DAV).

Leaves microphylls or mesophylls, symmetrical, typically narrow elliptic or lanceolate; apex acute or acuminate; base acute, obtuse, or rounded; organization of venation typically low to mid third rank, rarely (*C. micranthus*) second rank; marginal ultimate venation fimbriate or rarely looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or brachyparacytic; leaves glabrous or with trichomes scattered abaxially.

Two features unusual in the Phyllanthoideae appear in some *Cleistanthus* species. Members of sects. *Chartacei, Cleistanthus,* and *Leiopyxus* have a network of filiform fibers in the mesophyll giving the veins a frayed appearance. Only *Dicoelia* has similar fibers. Unique in the Phyllanthoideae are the two-armed dolabrate trichomes (Fig. 43) borne by species of sects. *Chartacei* and *Ferruginosi.*

Overall, most species of *Cleistanthus* included in this study are quite similar. The exceptions are the only representatives of sects. *Chartacei* (*C. cunninghamii*) and *Australes* (*C. micranthus*) that I examined. Both have strongly brochidodromous secondaries arising at higher angles than typical for the genus and less well organized higher order venation than most of the other species. The latter is particularly true of *C. micranthus* in which the tertiary veins are random reticulate rather than percurrent. The leaves of *C. cunninghamii* are not typical of *Chartacei* (Jablonsky, 1915); it is unfortunate that this is the only species in the section that I was able to obtain. On the basis of non-foliar characters, Jablonsky (1915) felt that *Australes* were rather isolated in *Cleistanthus,* which is corroborated by my evaluation of the leaves.

Typical leaves of the two genera in the Bridelieae do not seem to resemble each other very closely, but a connection between them can be seen through some of the higher ranked species of *Cleistanthus* and the fimbrial-veined groups of *Bridelia,* in agreement with the general interpretation, based on floral characters, that *Bridelia* is derived from *Cleistanthus*-like ancestry. After studying pollen exine sculpturing of four species each of *Bridelia* and *Cleistanthus,* Köhler (1965) suggested that *Bridelia* was derived polyphyletically from *Cleistanthus.* Examination of the pollen and leaves of more species in both genera might help clarify the relationship between them.

DICOELIEAE HURUSAWA

Dicoelia Benth. (OTU 25)

D. affinis J. J. Sm., Borneo: *Hallier 1255* (UC). Figures 44, 45.

Leaves mesophylls, symmetrical, narrow elliptic; apex acuminate; base acute-cuneate; organization of venation third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

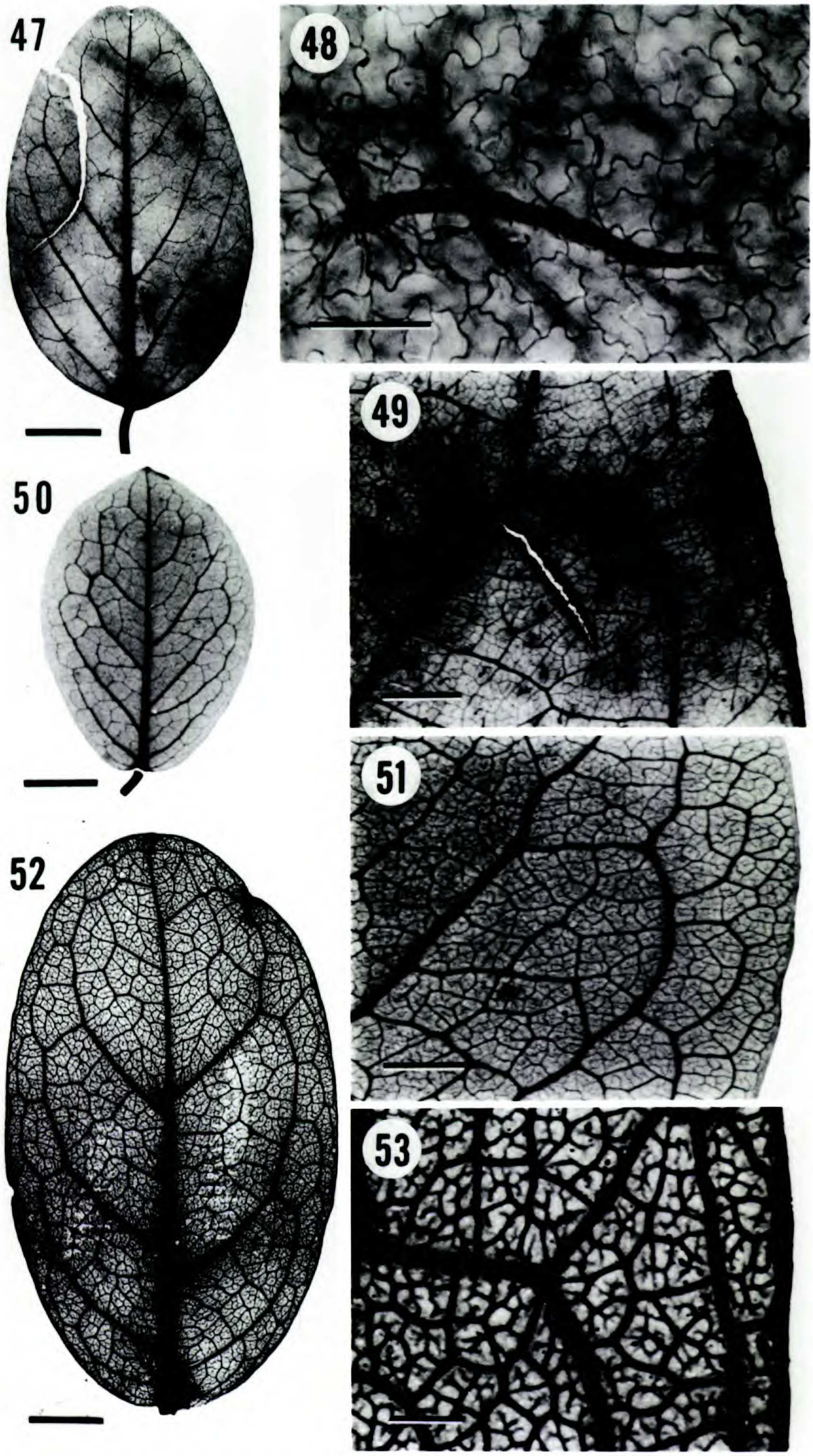
The leaves of *Dicoelia* share with some *Cleistanthus* species having filiform fibers in the mesophyll (Fig. 45). In general, however, the resemblance between these genera is not strong, which is consistent with the evidence from pollen morphology (Punt, 1962; Köhler, 1965) and wood anatomy (Metcalfe & Chalk, 1950). Indeed, as discussed above, foliar morphology suggests a relationship between *Dicoelia* and *Pentabrachium,* a relationship not before considered.

PORANTHEREAE (MUELL. ARG.) GRUNIG

Poranthera Rudge.

P. corymbosa Brongn., Australia: New South Wales, *Boorman (1903)* (UC). Figure 46.

Leaves simple, sessile, nanophylls, symmetrical, linear; apex acute; base symmetrical, the margins parallel; margin revolute; organization of venation low first rank, pinnate, kladodromous; primary vein massive, straight; secondary vein angle of origin very narrow acute and more or less uniform, thickness moderate to fine, course zig-zag and branched; higher vein orders not well resolved, forming an irregular reticulum of gradually thinning veins; marginal ultimate venation looped; areoles large and extremely irregular in size and shape; veinlets irregularly branched; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; adaxial epidermal cells rectangular, abaxial cells isodiametric, both arranged randomly, anticlinal walls undulate, abaxial cells with thickened ridges on the undulations, surfaces smooth; stomata abaxial, orientation random, stomatal index about 20%, brachyparacytic, the guard cells sunken and almost obscured by the subsidiary cells; trichomes and crystals none.



FIGURES 47–53. Leaves of *Andrachne* and *Spondianthus*.—47. *Andrachne chinense*.—48. Abaxial epidermis of *A. chinense*, showing unicellular trichome and anisocytic stomata (arrow).—49. *A. australis*.—50, 51. *A. phyllanthoides*.—52, 53. *Spondianthus preussii*. Bars equal 1 cm in Figures 47, 52; 5 mm in Figure 50; 1 mm in Figures 49, 51, 53; and 100 μm in Figure 48.

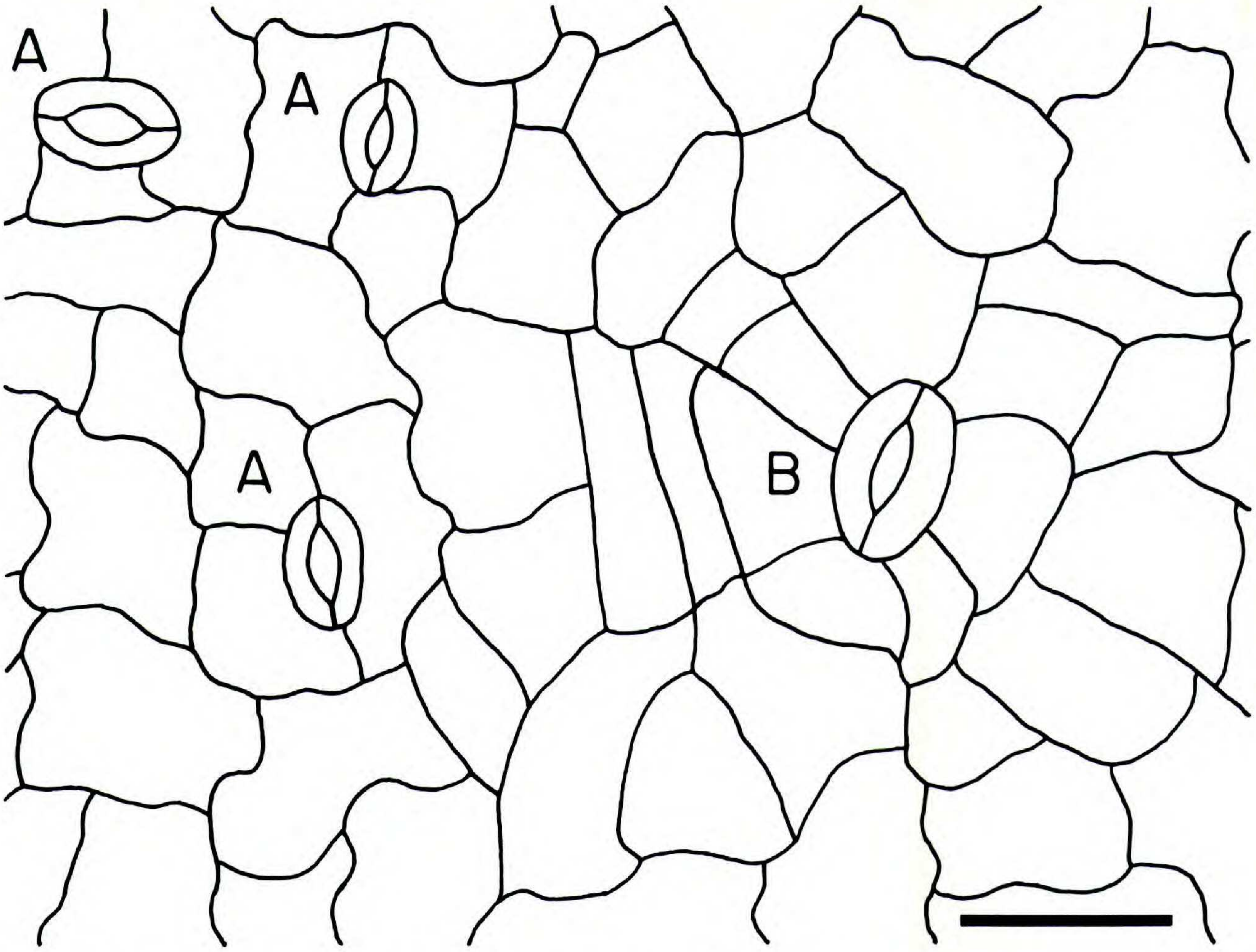


FIGURE 54. Abaxial epidermis of *Andrachne chinense*, showing anisocytic (A) and large anomocytic (B) stomata. Bar equals 100 μm.

Andrachne L.

Group 1 (OTU 26)
  Sect. *Arachne* (Neck.) Endl.
    A. australis Zoll., Annam: *Poilane 4755* (UC). Figure 49.
    A. chinense Bunge, India: Punjab, *Koelz 4423* (UC). Figures 47, 48, 54.
    A. cordifolia Muell. Arg., Pakistan: *Rodin 5378* (UC).
  Sect. *Phyllanthidia* (Didrichs.) Muell. Arg.
    A. microphylla (Lam.) Baill., Peru: *Sagastegni & Cabanillas 8738* (DAV).

Leaves microphylls, symmetrical, ovate; apex attenuate or rounded to emarginate; base acute, obtuse, or rounded; organization of venation high second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; typical stomata anisocytic (Fig. 48), large anomocytic "water stomata" also present (Fig. 54); trichomes scattered on abaxial epidermis, denser beneath lower order veins, in some species also scattered on adaxial epidermis.

Group 2 (OTU 27)
  Sect. *Phyllanthopsis* (Scheele) Muell. Arg.
    A. arida (Warnock & M. C. Johnst.) Webster, U.S.A.: Texas, *Butterwick & Lott 3582* (DAV).
    A. phyllanthoides (Nutt.) Muell. Arg., U.S.A.: Missouri, *Palmer 45338* (UC). Figures 50, 51.

Leaves nanophylls, symmetrical, elliptic; apex obtuse; base acute or rounded; organization of venation low second rank; marginal ultimate venation looped (*A. phyllanthoides*) or incomplete (*A. arida*); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes scattered on both surfaces, densest beneath midrib and secondaries.

My anatomical observations generally agree with those of Rothdauscher (1896), who included *A. chinensis, A. cordifolia,* and *A. phyllanthoides* among the seven species he studied. He did not, however, report the large anomocytic stomata I found in sects. *Arachne* and *Phyllanthidia.*

The members of this tribe are perennial herbs or subshrubs, many extending into drier and more temperate habitats than most other phyllanthoids (Pax & Hoffmann, 1922; Webster, 1967). Surprisingly, the rank of the venation of the two species in *Andrachne* sect. *Phyllanthopsis* remains comparatively high for such xeromorphic leaves, which generally show a regression in organization below the leaves of their more mesophytic relatives (Hickey, 1971). The strikingly low rank of the leaves of *Poranthera* reflects the extremely xerophytic nature of this Australian endemic and reveals nothing about its relationships.

Section *Phyllanthopsis* has been repeatedly transferred between *Savia* and *Andrachne* (cf. Mueller, 1866; Pax & Hoffmann, 1922; Webster, 1967). The anisocytic stomata and undulate anticlinal walls on the epidermal cells suggest that *Phyllanthopsis* is better included in *Andrachne*, the conclusion both Punt (1962) and Köhler (1965) came to when studying the pollen. The venation of *Phyllanthopsis* also appears somewhat more organized than would be expected from a xeric *Savia* derivative, being more comparable to other *Andrachne* sections.

SPONDIANTHEAE WEBST.

Spondianthus Engl. (OTU 28)

S. preussii Engl., Cameroons: *Zenker 563* (CAS), Ghana: *Oldeman 818* (MO), Congo: *Louis 13728* (UC). Figures 52, 53.

Leaves mesophylls, symmetrical, wide elliptic; apex rounded; base rounded; organization of venation second rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata paracytic.

The paracytic stomata and tanniniferous epidermal cells would associate *Spondianthus* with the Antidesmeae, in which the second rank venation, few secondaries enclosing large intercostal areas, and random-reticulate tertiaries with a tendency to ramify admedially would be anomalously primitive. I am inclined to agree with Webster's (1975) placement of this genus in its own tribe near the Antidesmeae, of which it may be the primitive sister group (Levin, in press).

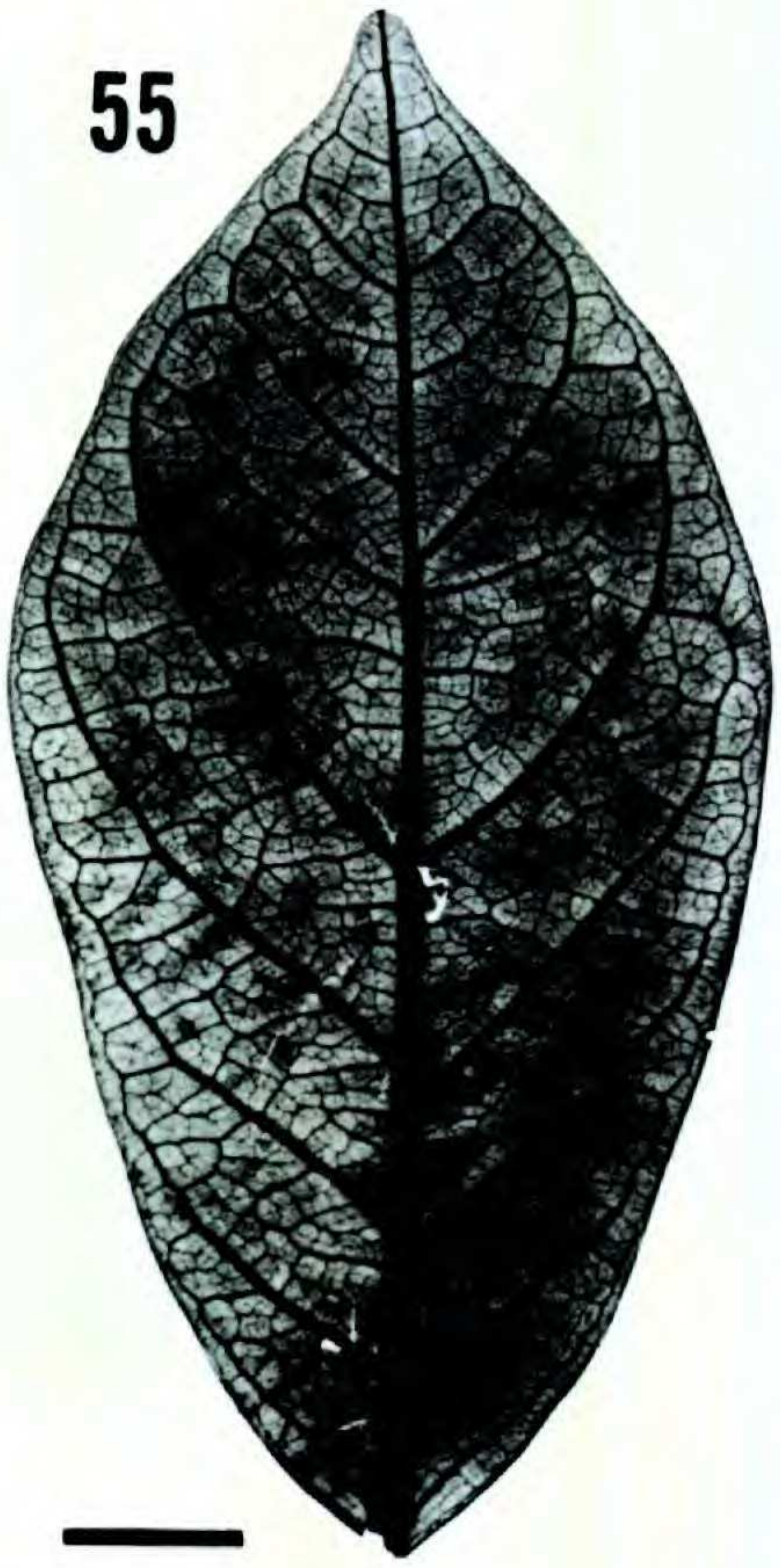
ANTIDESMEAE (ENDL.) HURUSAWA

Antidesma L.

Group 1 (OTU 29)
  Sect. *Roxburghiana* Pax & K. Hoffm.
    A. vogelianum Muell. Arg., Tanganyika: *Tanner 2564* (UC).
  Sect. *Venosa* Pax & K. Hoffm.
    A. henryi Hemsl., China: Hainan, *Tsang et al. 23* (UC).
    A. japonicum Sieb. & Zucc., Taiwan: *Tanaaka & Shimada 13570* (UC).
    A. venosum Tul., Tanganyika: *Tanner 3424* (UC). Figure 55.
Group 2 (OTU 30)
  Sect. *Laciniata* Pax & K. Hoffm.
    A. laciniatum Muell. Arg., Congo: *Louis 11467* (MO).
  Sect. *Venosa* Pax & K. Hoffm.
    A. cuspidatum Muell. Arg., Sumatra: *Toroes 5296* (UC).
    A. delicatulum Hutch., China: Chekiang, *Ching 2038* (CU). Figures 57, 58.
    A. gracile Hemsl., China: Kwangtung, *Tsang 21272* (UC).
    A. maclurei Merr., China: Hainan, *Fung 20210* (UC).
    A. membranaceum Muell. Arg., Belgian Congo: *Louis 6088* (UC), Ghana: *Hall & Abbiw 43391* (GC).
Group 3 (OTU 31)
  Sect. *Tetrandra* Pax & K. Hoffm.
    A. angusanense Elm., Philippines: *Ramos & Pasgasio (1919)* (UC).
    A. digitaliforme Tul., Philippines: *McClure 15967* (UC).
    A. fructifera Elm., Philippines: *Ramos (1915)* (UC). Figure 56.
Group 4 (OTU 32)
  Sect. *Montana* Pax & K. Hoffm.
    A. bunius Spreng., China: Kwangtung, *Tsiang Ying 1013* (UC).
    A. insulare Gillespie, Fiji: *Smith 656* (UC).
    A. platyphyllum Mann, U.S.A.: Hawaii, *Meinecke (1933)* (UC).
Group 5 (OTU 33)
  Sect. *Velutinosa* Pax & K. Hoffm.
    A. fordii Hemsl., Hong Kong: *Chun 5089* (UC).
Group 6 (OTU 34)
  Sect. *Ghaesembilla* Pax & K. Hoffm.
    A. ghaesembilla Gaertn., China: Hainan, *Tsang 15564* (UC), Sumatra: *Toroes 4828* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic, narrow elliptic, or narrow obovate; apex typically acuminate or acute, less typically obtuse or rounded; base acute, obtuse, or rounded; organization of venation low to mid third

55



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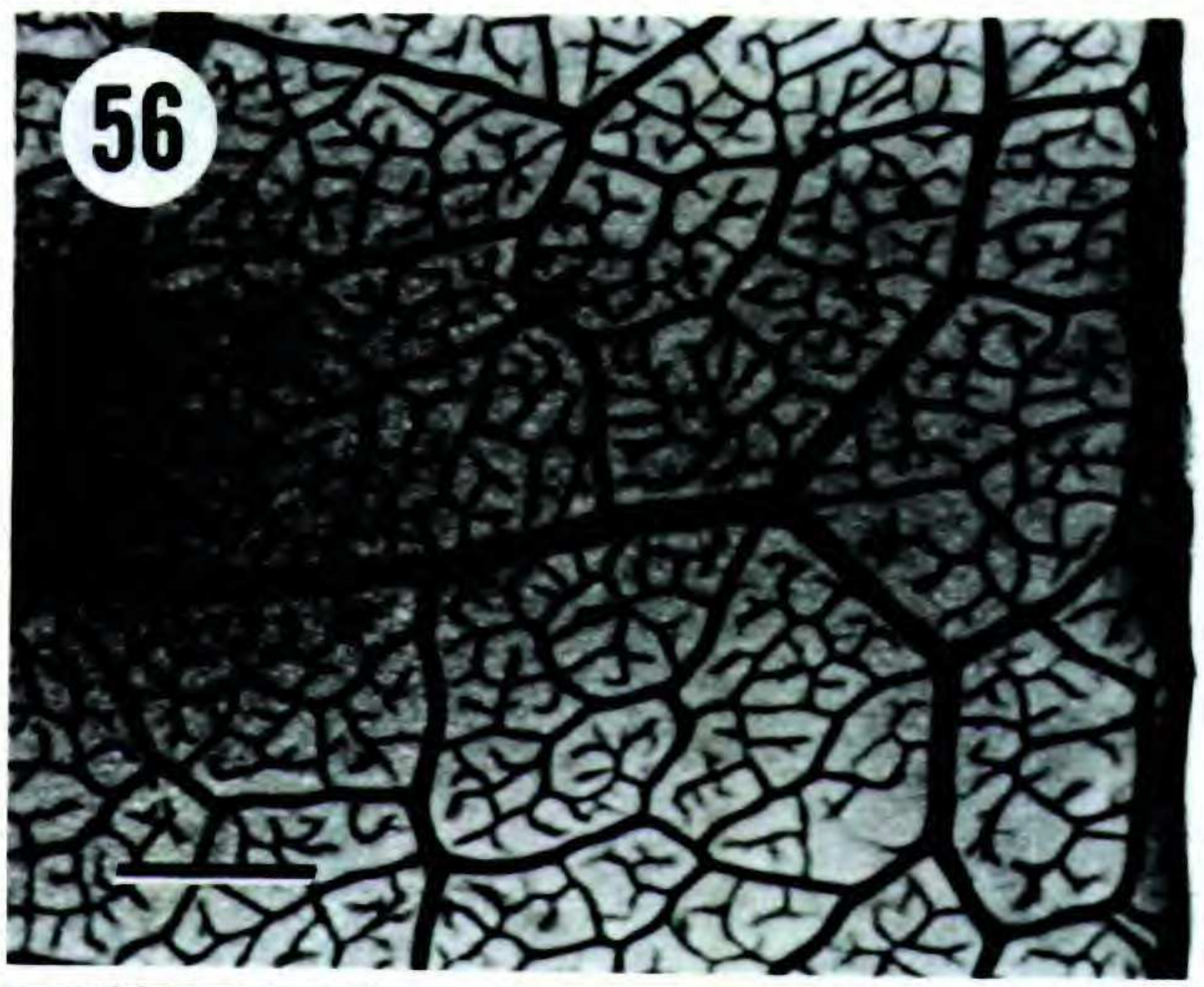

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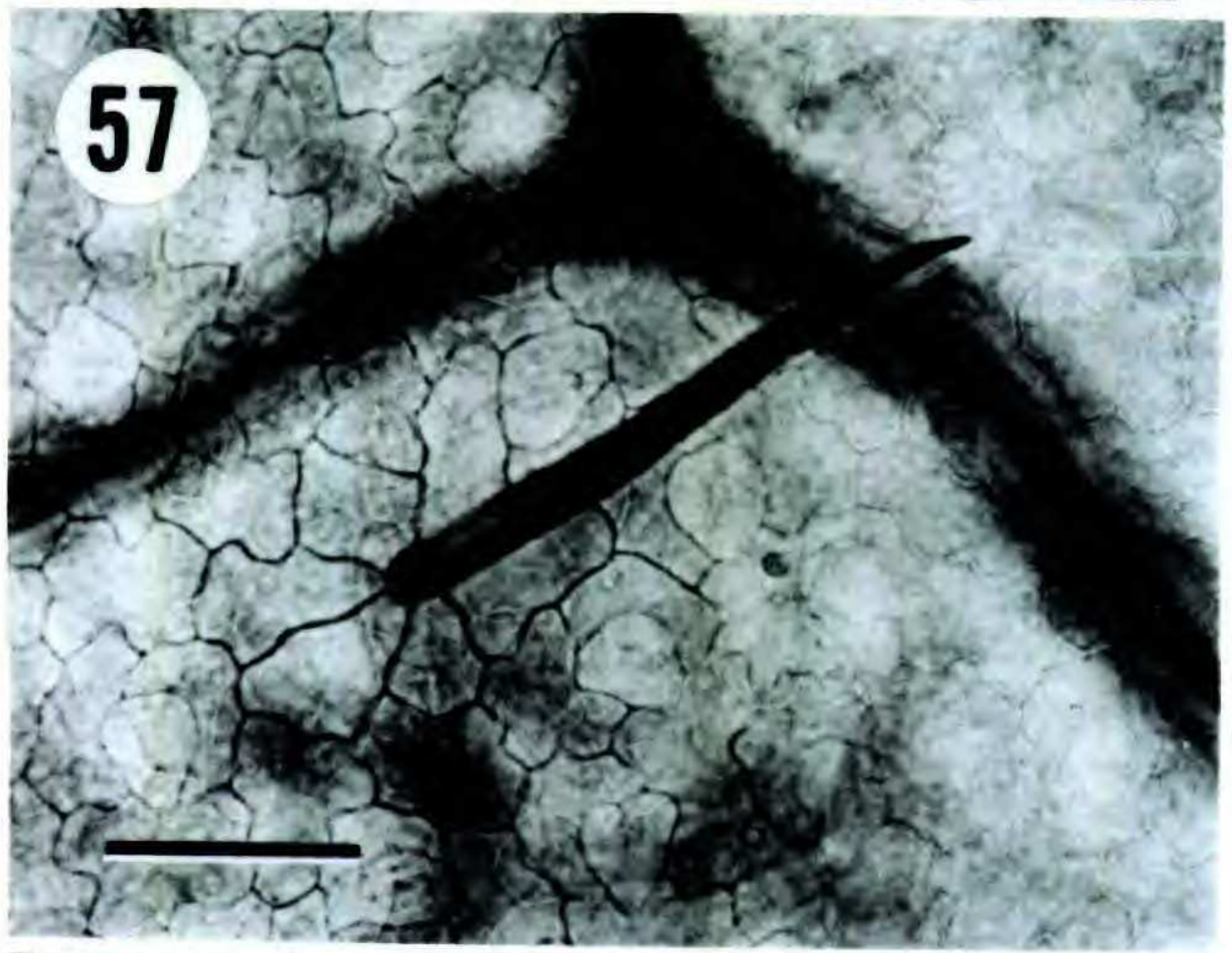

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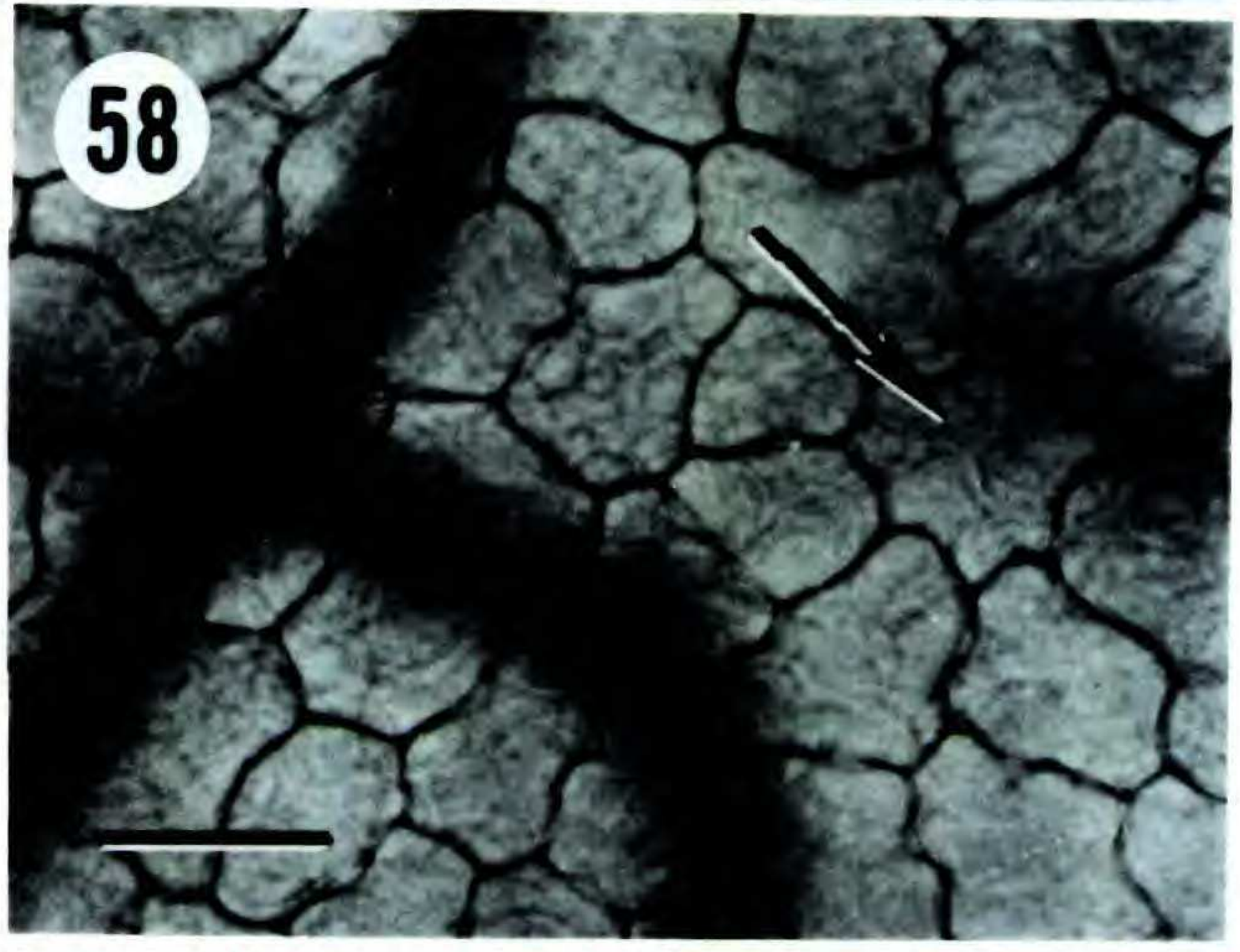

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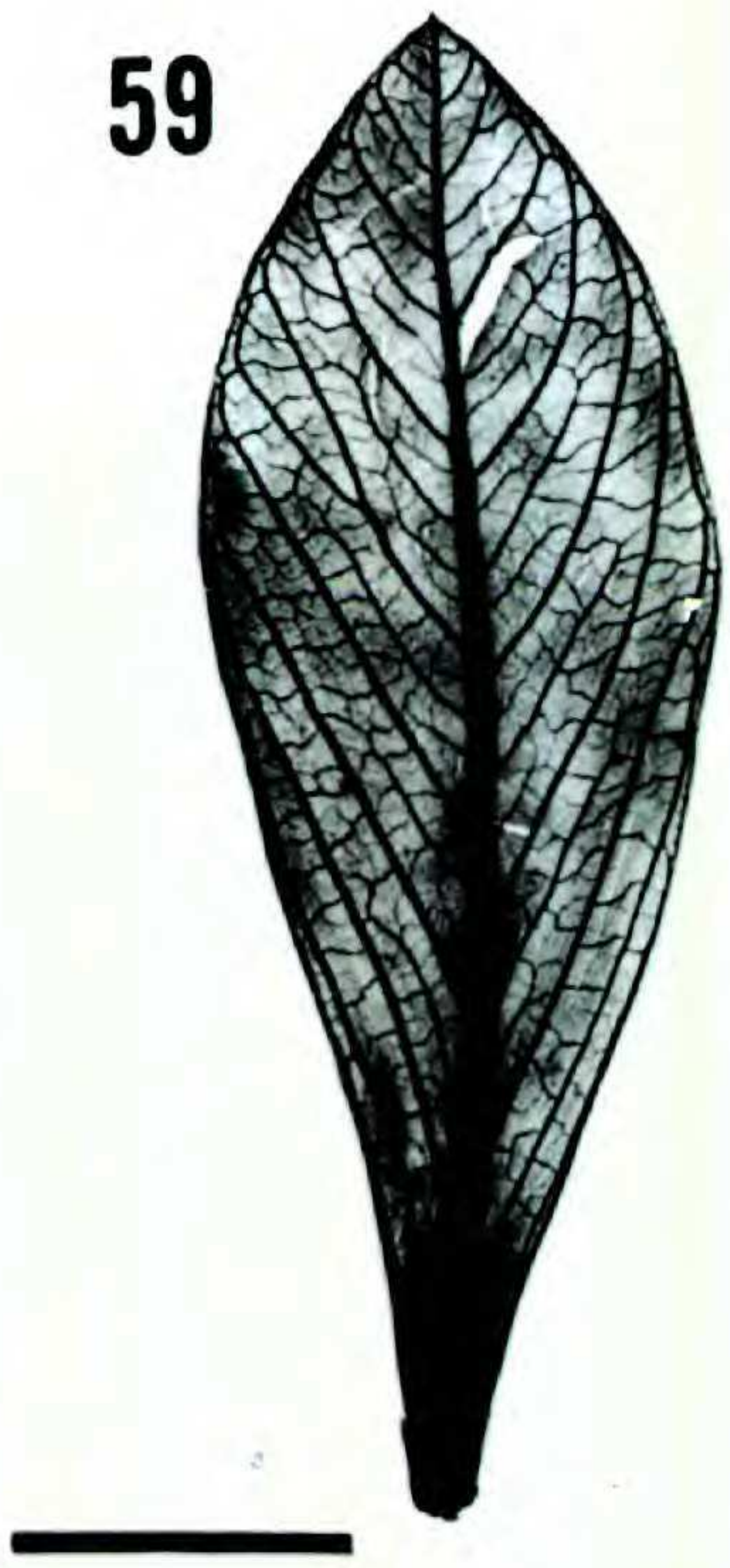

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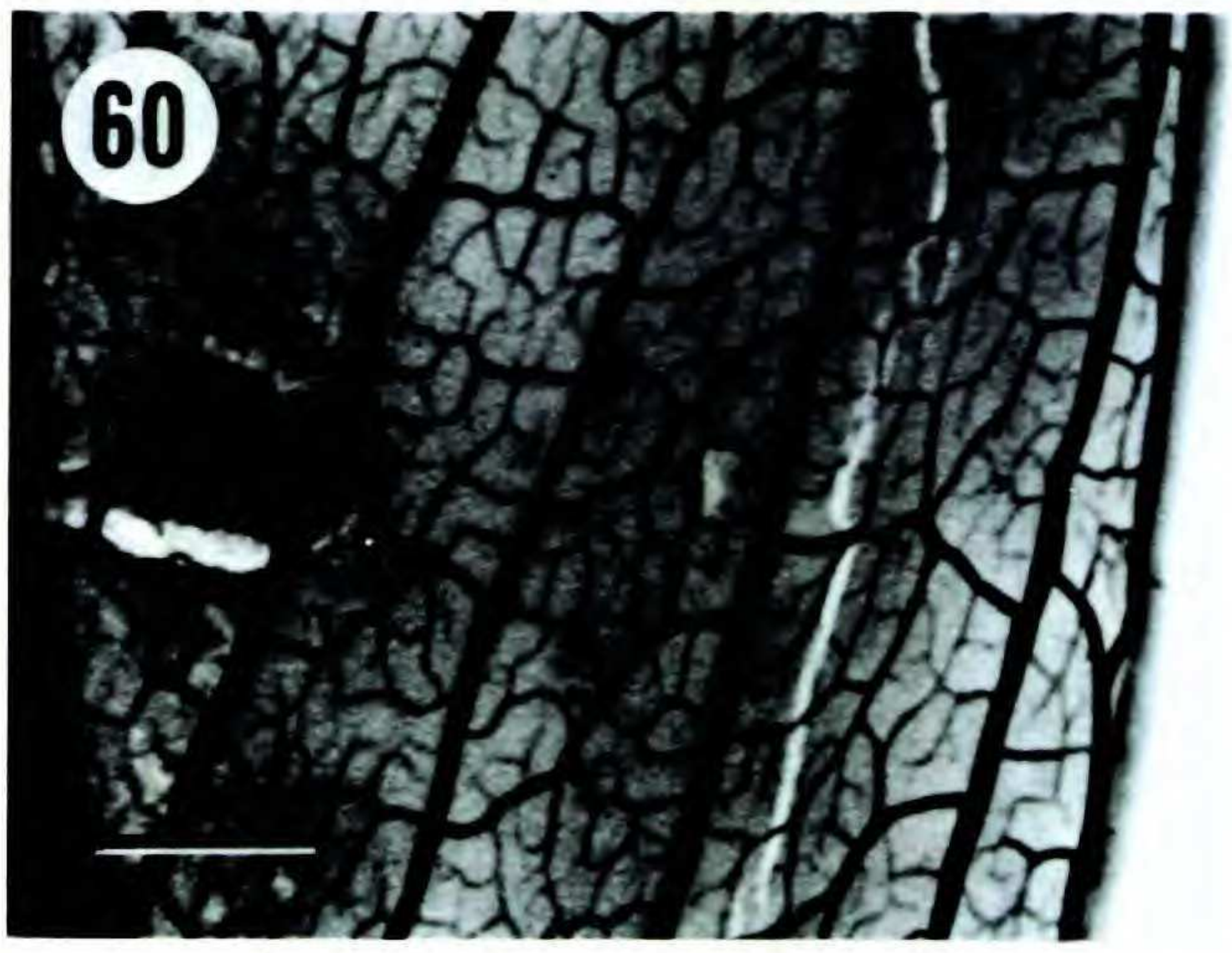
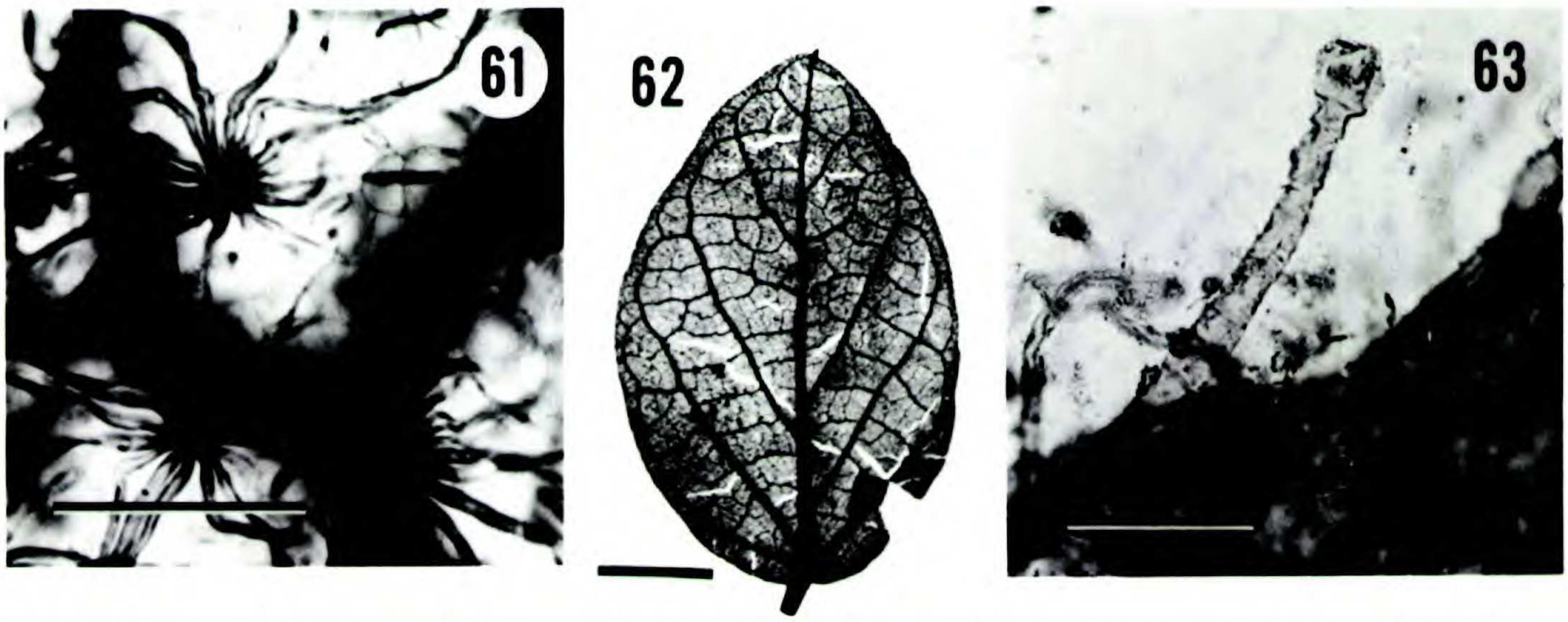


FIGURES 55–60. Leaves of *Antidesma* and *Celianella*.—55. *Antidesma venosum*.—56. *A. fructifera*.—57. Abaxial epidermis of *A. delicatulum*, showing unicellular trichome.—58. Adaxial epidermis of *A. delicatulum*, showing tanniniferous epidermal cell (arrow).—59, 60. *Celianella montana*. Bars equal 1 cm in Figures 55, 59; 1 mm in Figures 56, 60; 100 μm in Figure 57; and 50 μm in Figure 58.



FIGURES 61–63. Leaves of *Hyeronima* and *Leptonema*.—61. Peltate trichomes of *Hyeronima alchornioides*.—62. *Leptonema venosa*.—63. Multicellular trichome on margin of leaf of *L. venosa*. Bars equal 5 mm in Figure 62 and 100 μm in Figures 61, 63.

rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes typically present at least beneath low order veins and in many species also scattered on abaxial intercostal areas, less typically over low order veins or the leaves glabrous.

My anatomical observations agree with Rothdauscher (1896) and Gaucher (1902) except in one respect: they reported that stomata were restricted to the abaxial epidermis in all 11 species they examined, including *A. ghaesembilla*. In the two specimens of this species that I examined, I found a few (stomatal index 1–2%) stomata in the adaxial epidermis.

Celianella Jabl. (OTU 35)
C. montana Jabl., Venezuela: Amazonas, *Maguire & Maguire 35071* (US). Figures 59, 60.

Leaves microphylls, symmetrical, oblanceolate; apex acute with a small apiculum; base acute-decurrent; organization of venation low third rank; secondary veins quite numerous and closely spaced, alternating with intersecondaries; tertiary veins percurrent but sinuous; marginal ultimate venation formed by basal secondaries in lower portion of leaf, looped above; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Hyeronima Fr. Allem. (OTU 36)
H. alchorneoides Fr. Allem., Venezuela: Amazonas, *Krukoff 5032* (UC). Figure 61.
H. guatemalensis D. Sm., Costa Rica: *Stork 4213* (UC).
H. poasana Standl., Costa Rica: *Smith 2012* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic or obovate; apex acuminate; base acute or rounded; organization of venation low to mid third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic; unicellular trichomes beneath primary and secondaries; peltate trichomes scattered on adaxial epidermis, densely covering abaxial epidermis.

My anatomical observations agree with those of Rothdauscher (1896).

Leptonema A. Juss. (OTU 37)
L. venosum (Poir.) Juss., Madagascar: *Decary 13624* (P). Figures 62, 63.

Leaves nanophylls to microphylls, symmetrical, wide elliptic; apex obtuse and cuspidate; base rounded; organization of venation third rank; marginal ultimate venation looped; terminal tracheids swollen; bundle sheath of higher order veins parenchymatous; stomata paracytic; unicellular trichomes scattered on adaxial epidermis, especially beneath low order veins; multicellular, uniseriate trichomes with single-celled glandular heads scattered beneath lower order veins and dense on margins of blade.

Thecacoris A. Juss. (OTU 38)
T. gymnogyne Pax, Cameroons: *Zenker 23* (CAS).

T. leptobotrya (Muell. Arg.) Brennan, Cameroons: *Olorunfemi 30638* (DAV).
T. trichogyne Muell. Arg., Rhodesia: *Brenan & Greenway 8031* (EAH).

Leaves microphylls to mesophylls, symmetrical, obovate or elliptic; apex acute to acuminate; base acute; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or occasionally parallelocytic; trichomes dense beneath low order veins and scattered on adaxial epidermis.

The central genera of the Antidesmeae, *Antidesma, Hyeronima,* and *Thecacoris,* have extremely similar leaves, which can be recognized architecturally by their regularly spaced secondaries enclosing more or less parallel-sided intercostal areas and very weakly percurrent tertiaries. The additional combination of paracytic stomata and tanniniferous epidermal cells confirms the identification of members of this tribe. Airy Shaw's (1973) resurrection of the family Stilaginaceae for *Antidesma* receives no support from foliar morphology; his suggestion of a relationship to the Icacinaceae directly contradicts the evidence, for the latter have anomocytic or anisocytic stomata (Metcalfe & Chalk, 1950), fewer, more curving secondaries, more strongly percurrent tertiaries, and generally more orthogonal and organized higher order venation (pers. observ.). In fact, the leaves of some sections of *Antidesma* and *Hyeronima* are so similar that if it were not for the peltate trichomes of *Hyeronima,* one could not reliably distinguish leaves of the two genera.

The other two genera that I examined, *Celianella* and *Leptonema,* have leaves that depart considerably from the typical architecture of the tribe. Both, however, share the tanniniferous epidermal cells and paracytic stomata characteristic of the Antidesmeae, suggesting that they do, in fact, belong here. Pollen evidence supports this placement of *Leptonema* (Köhler, 1965). The alternative treatment, followed by most authors, places *Leptonema* among the genera included in Webster's Phyllantheae. Only the uniseriate, multicellular trichomes with unmodified bases argue strongly for this relationship. However the spherical glandular cell at the apex contrasts markedly with the blunt or tapering, non-glandular terminal cell in the Phyllantheae (cf. Figs. 63, 100, 102). Both phenetic and cladistic analyses of leaf characters place *Leptonema* with the Antidesmeae (Levin, 1986 and in press).

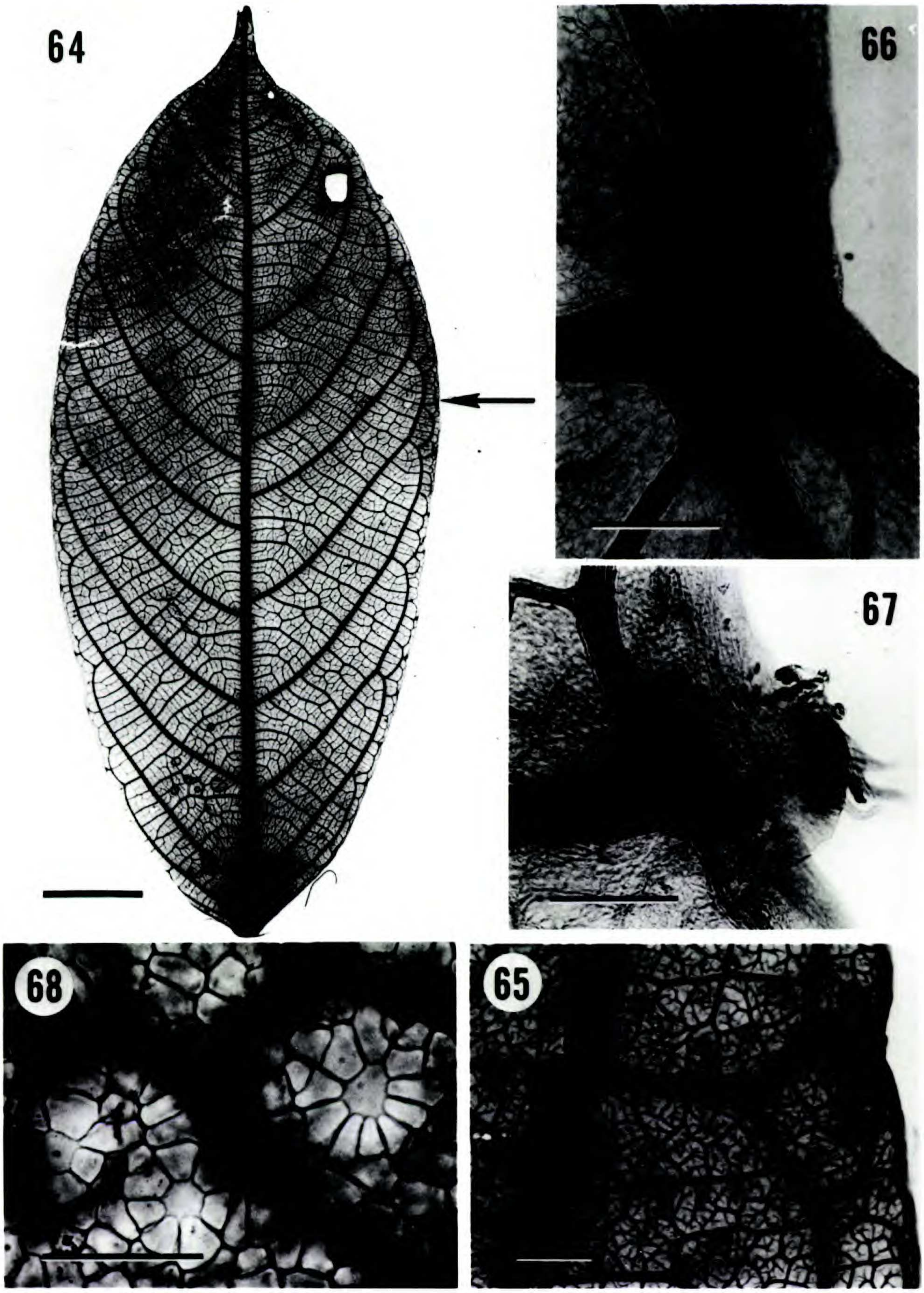
Celianella, described by Jablonsky in 1965, remains poorly known, and its wood and pollen have never been described. Even more so than *Leptonema,* its leaves contrast with the other members of the Antidesmeae. No other phyllanthoids exhibit similar architecture, with numerous, closely spaced secondaries typically alternating with intersecondaries, sinuous, percurrent tertiaries, and few vein orders. However, these features may result from modification of the basic Antidesmeae-type leaf during evolution of the coriaceous, sub-succulent leaves of this genus, a possibility supported by cladistic analysis (Levin, in press).

APORUSEAE (LINDL. EX MIQ.) AIRY SHAW

Aporusa Bl. (OTU 39)
A. aurita (Tul.) Miq., Philippines: *Salvoza (1924)* (UC). Figure 67.
A. chinensis (Champ.) Merr., China: Hainan, *Gressitt 876* (UC).
A. frutescens Blume, British N Borneo: *Ramos 1364* (UC). Figures 64, 65.
A. lanceolata Hance, China: Kwangtung, *Chun 6391* (UC). Figure 66.
A. microcalyx Hassk., Indonesia, *cult. Hort. Bog.* (UC 234706).
A. sphaeridophora Merr., Philippines: *Cenabre (1924)* (UC).
A. symplocifolia Merr., Philippines: *Loher 14360* (UC). Figure 68.
A. villosa (Lindl.) Baill., Siam: *Rock 1673* (UC).

Leaves microphylls to mesophylls, symmetrical, lanceolate, ovate, or elliptic; apex acuminate to caudate or obtuse; base acute, obtuse, or rounded; organization of venation low to mid third rank; marginal ultimate venation looped or partially incomplete; terminal tracheids normal or rarely (*A. sphaeridophora*) swollen; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes typically present at least beneath midrib and secondaries, may also be scattered on abaxial epidermis and over midrib and secondaries.

My anatomical observations generally agree with those of Rothdauscher (1896) and Gaucher (1902); as Rothdauscher remarked, the tanniniferous cells in the adaxial epidermis are remarkably large in *Aporusa* and the other genera in the Aporuseae.



Figures 64–68. Leaves of *Aporusa*.—64, 65. *A. frutescens*. Arrow indicates marginal gland.—66. Marginal gland of *A. lanceolata*.—67. Marginal gland of *A. aurita*.—68. Adaxial epidermis of *A. symplocifolia*, with tanniniferous epidermal cells. Bars equal 2 cm in Figure 64; 1 mm in Figure 65; 200 μm in Figures 66, 67; and 100 μm in Figure 68.

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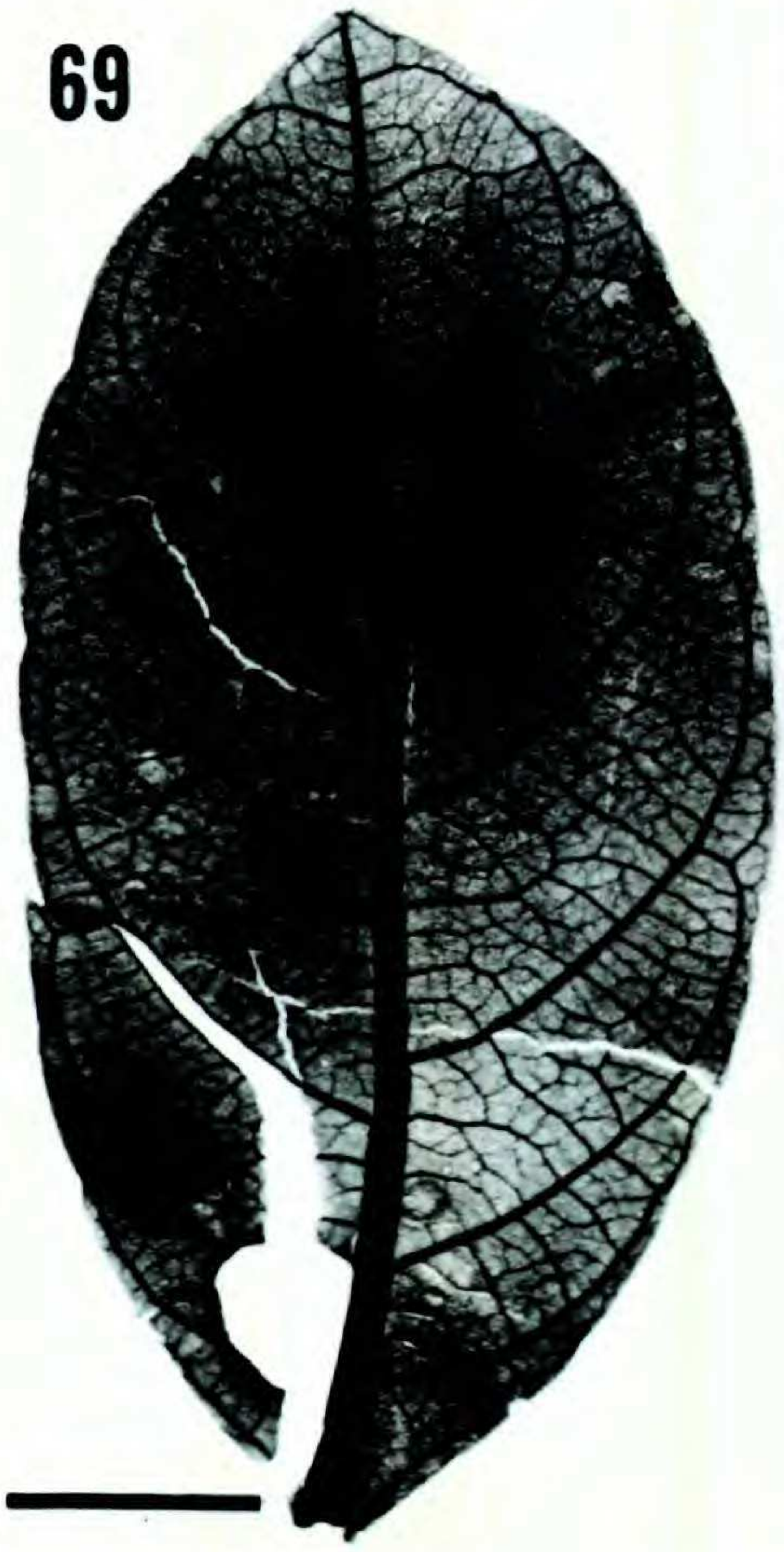

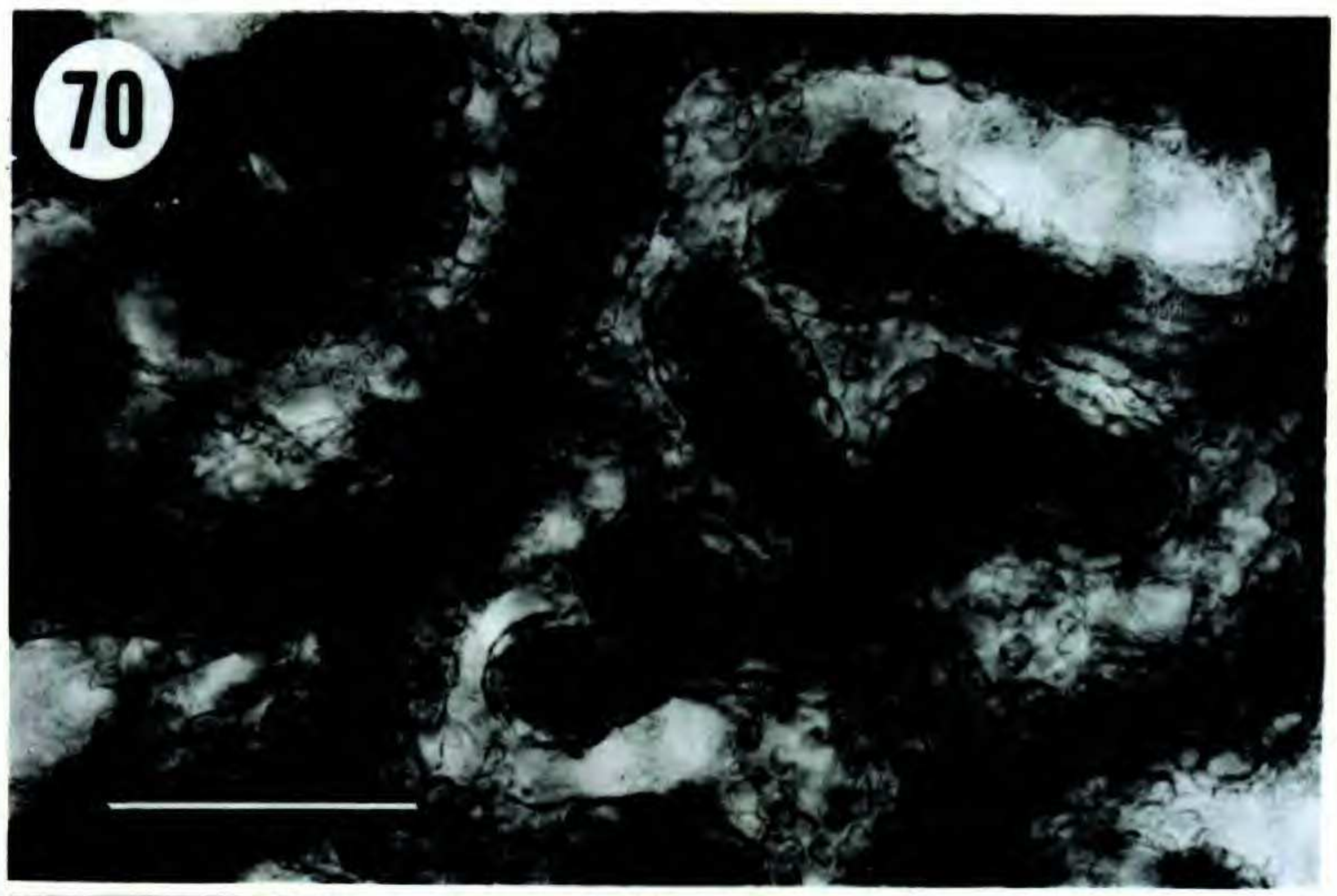

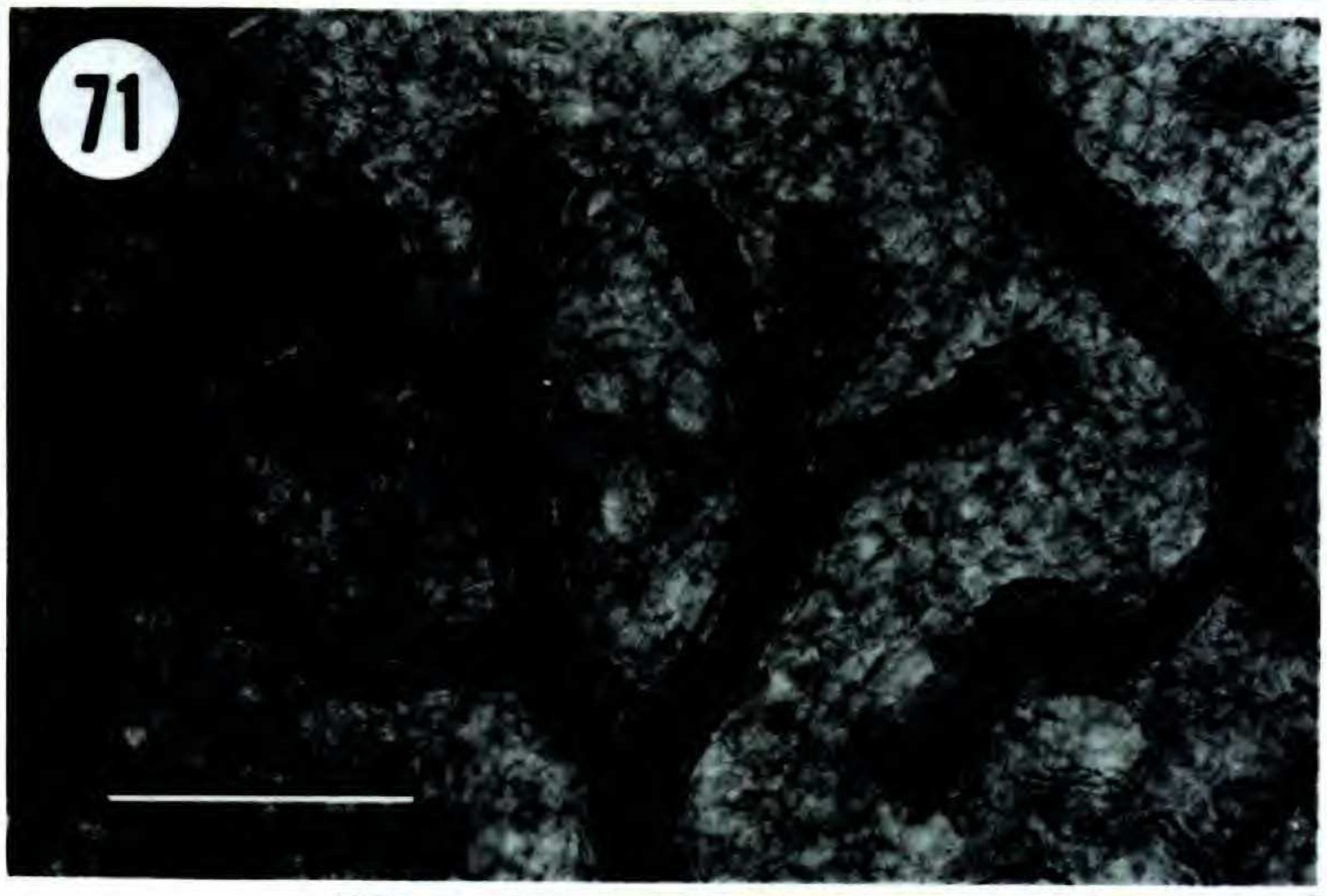

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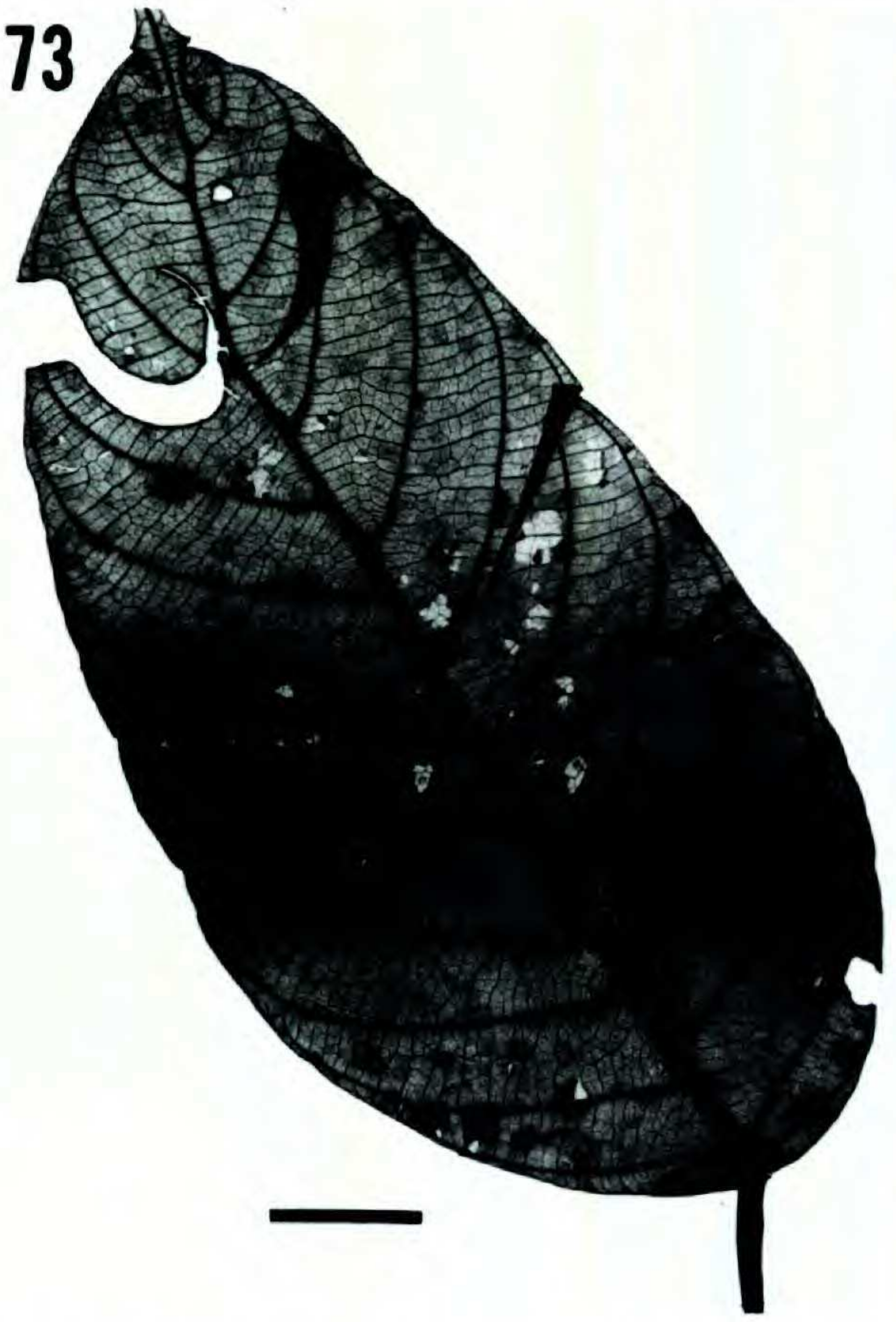
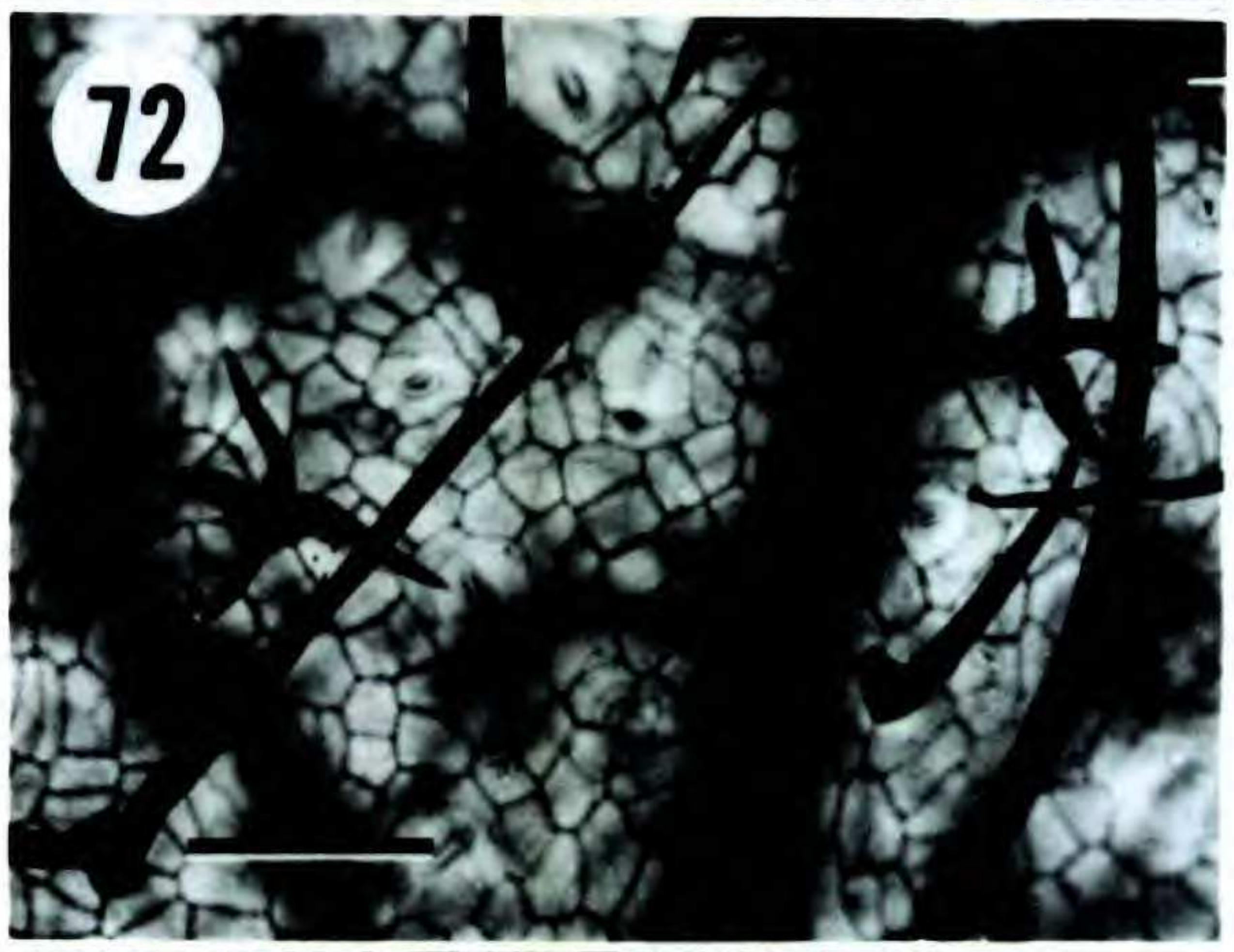
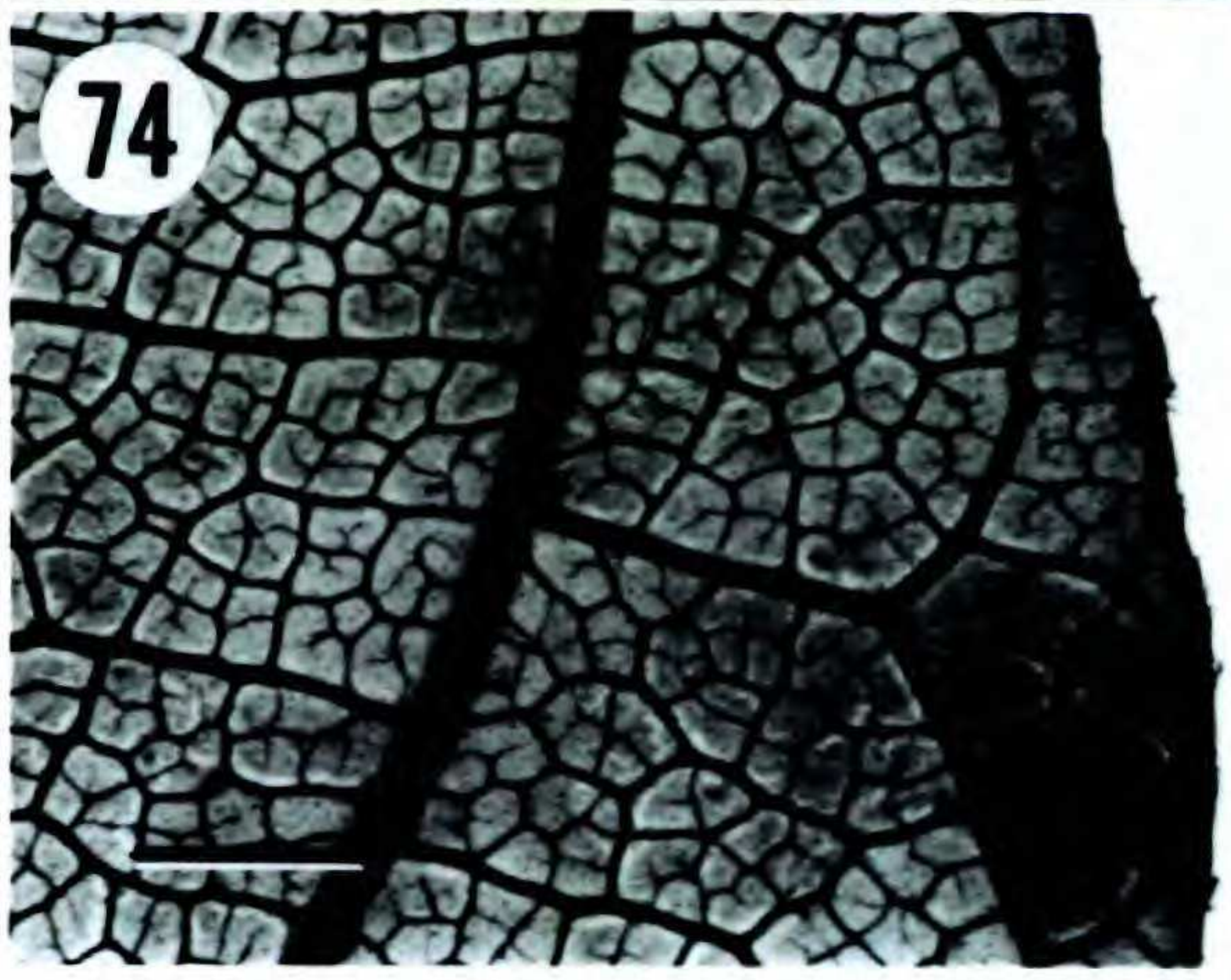






FIGURES 69–74. Leaves of *Ashtonia, Baccaurea,* and *Didymocistus.*—69, 70. *Ashtonia praeterita.*—71. *A. whitmorei.*—72. Abaxial epidermis of *Baccaurea deflexa,* with solitary and tufted trichomes.—73, 74. *Didymocistus chrysadenius.* Bars equal 2 cm in Figure 73; 1 cm in Figure 69; 1 mm in Figure 74; 200 μm in Figures 70, 71; and 100 μm in Figure 72.

Ashtonia Airy Shaw (OTU 40)
A. praeterita Airy Shaw, Malaya: *Everett KEP 104934* (A). Figures 69, 70.
A. whitmorei Airy Shaw, Malaya: *Stone 8654* (A). Figure 71.

Leaves microphylls, symmetrical, elliptic; apex obtuse; base obtuse; organization of venation mid third rank; marginal ultimate venation mostly incomplete; terminal tracheids more or less normal (*A. whitmorei*) or swollen (*A. praeterita*); bundle sheath of higher order veins lightly (*A. whitmorei*) or heavily (*A. praeterita*) sclerified; stomata anisocytic; trichomes scattered beneath midrib.

If the specimens I examined are representative, the degree of enlargement of the terminal tracheids and of the sclerification of the bundle sheath allow one to distinguish easily between leaves of the two species (Figs. 70, 71).

Baccaurea Lour.
- Group 1 (OTU 41)
  - Sect. *Calyptroon* (Miq.) Muell. Arg.
    - *B. wilkesiana* Muell. Arg., Fiji: *Smith 9692* (UC).
  - Sect. *Everettiodendron* (Merr.) Pax & K. Hoffm.
    - *B. bracteata* Muell. Arg., Singapore: *Ridley 1893* (UC).
    - *B. deflexa* Muell. Arg., British N Borneo: *Elmer 21118* (UC). Figure 72.
    - *B. philippinensis* Merr., Philippines: *Wenzel 3007* (UC).
- Group 2 (OTU 42)
  - Sect. *Pierardia* (Roxb.) Muell. Arg.
    - *B. obtusa* A. C. Smith, Fiji: *Smith 1780* (UC), *Webster & Hildreth 14140* (DAV).
    - *B. pendula* Merr., British N Borneo: *Elmer 21290* (UC).
    - *B. racemosa* (Reinw.) Muell. Arg., British N Borneo: *Elmer 21195* (UC).
- Group 3 (*Dubiae*) (OTU 43)
  - *B. cauliflora* Lour., China: Hainan, *Fung 20024* (UC).
- Group 4 (OTU 44)
  - Sect. *Isoandrion* (Baill.) Muell. Arg.
    - *B. stylaris* Muell. Arg., Fiji: *Smith 8060* (UC), *Webster & Hildreth 14046* (DAV).

Leaves microphylls to mesophylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, or obtuse; base acute-decurrent, acute, obtuse, or rounded; organization of venation third rank; marginal ultimate venation looped or partially incomplete; terminal tracheids normal; bundle sheath of higher order veins lightly or heavily sclerified; stomata anisocytic, rarely the smallest cell divided again parallel to the guard cells; trichomes typically of two lengths, the longer solitary, the shorter solitary or tufted in groups of 2–5(–8), both scattered beneath lower order veins or generally on abaxial epidermis (Fig. 72), or rarely the leaves glabrous.

Rothdauscher's (1896) and Gaucher's (1902) anatomical observations agree with mine.

Didymocistus Kuhlm. (OTU 45)
D. chrysadenius Kuhlm., Peru: *Asplund 14760* (CAS). Figures 73, 74.

Leaves mesophylls, symmetrical, ovate-elliptic; apex acuminate; base rounded; organization of venation fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic; trichomes of two types, the longer ones solitary, scattered beneath midrib and dense abaxially in junction of midrib and secondaries, the shorter ones tufted in groups of 3–15, scattered on both surfaces but denser abaxially and beneath veins; lower epidermis densely covered with sessile, disk-shaped glands.

Maesobotrya Benth. (OTU 46)
M. barteri (Baill.) Hutch., Liberia: *Leeuwenberg 4851* (MO).
M. bipindensis (Pax) Hutch., Cameroons: *Zenker 2598* (MO).
M. dusenii (Pax) Hutch., Cameroons: *Zenker (1906)* (CAS), *Olorunfemi s.n.* (DAV 47305).
M. floribunda Benth., Congo: *Leonard 251* (UC).
M. pynaertii (De Wild.) Pax & Hoffm., Congo: *Leonard 334* (MO).
M. staudtii (Pax) Hutch., Congo: *Donie 2113* (MO), Cameroons: *Zenker 568* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic or oblong; apex long acuminate; base acute or obtuse; organization of venation mid third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal or somewhat swollen (*M. dusenii* and *M. floribunda*); bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes scattered or dense beneath midrib and secondaries and on margin, may also be scattered on abaxial epidermis.

Among the Aporuseae, *Maesobotrya* comes the closest to being toothed, with species such as *M.*

floribunda and *M. staudtii* having denticulate margins.

Protomegabaria Hutch. (OTU 47)
P. stapfiana Hutch., Ghana: *Enti FHI 8167* (G).

Leaves mesophylls, symmetrical, elliptic; apex acute; base acute; organization of venation mid third rank; marginal ultimate venation looped to partially incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes dense beneath midrib and secondaries.

Richeria Vahl. (OTU 48)
R. australis Muell. Arg., Santa Catarina: *Reitz & Klein 4044* (UC).
R. grandis Vahl., Venezuela: *Wurdack & Monachino 41152* (UC).
R. obovata (Muell. Arg.) Pax & Hoffm., Matto Grosso: *Irwin & Soderstrom 6445* (NY).
R. racemosa (Poepp. & Endl.) Pax & Hoffm., Venezuela: *Maquire & Politi 28440* (DAV).

Leaves mesophylls, symmetrical, obovate; apex acute or obtuse; base acute or obtuse; organization of venation mid third rank; marginal ultimate venation looped to partially incomplete; terminal tracheids normal or swollen; bundle sheath of higher order veins parenchymatous; stomata basically anisocytic, but with a tendency toward being helicocytic; trichomes scattered or dense beneath midrib and proximal portions of secondaries, or the leaves glabrous.

My observations generally agree with those of Rothdauscher (1896), Gaucher (1902), and Hayden (1980), except that Hayden considered the stomata to be anomocytic. Indeed, as Rothdauscher noted, the number of subsidiary cells surrounding each pair of guard cells varies between three and four; this variation, with the concomitant variation in cell size and shape, may suggest the anomocytic pattern. I, however, interpret the stomatal complex as developing in a spiral pattern, described by Payne (1970) as giving rise to either anisocytic or helicocytic stomata.

The Aporuseae were first recognized as a distinct group by Köhler (1965), who considered the group closely related to the Antidesmeae, in which the genera had been scattered by earlier authors. Foliar morphology certainly supports this treatment. The architecture of the two tribes is quite similar, but the Aporuseae can be separated on the basis of having much larger tanniniferous cells in the epidermis, anisocytic rather than paracytic stomata, and marginal glands. Also the level of venational organization tends to be higher in the Aporuseae. Cladistic analysis of the leaf characters suggests that the Aporuseae are specialized derivatives of the Antidesmeae (Levin, in press).

The marginal glands, located either on the ends of small teeth or in the sinuses of small crenulations, may represent remnants of the theoid teeth found in *Bischofia, Drypetes,* and *Putranjiva.* However, as the Aporuseae appear not to be particularly closely related to these genera but to be derived from entire-leaved ancestors, the alternative hypothesis that the glands have evolved *de novo* may be more parsimonious (Levin, in press).

Two genera placed in the Aporuseae by Webster (1975) do not conform completely with the typical foliar morphology of the tribe. Of these, *Protomegabaria* departs only in lacking marginal glands. Köhler (1965) commented that pollen characters placed *P. stapfiana* in the Aporuseae, but *P. macrophylla* resembled the Antidesmeae. Perhaps *Protomegabaria* represents an intermediate between these tribes. Alternatively, the glands may be secondarily absent; some other genera have glandless species (e.g., *Richeria obovata*). It would be worthwhile to examine leaves of *P. macrophylla* to determine the stomatal type and size of the tanniniferous epidermal cells.

In contrast, leaves of *Didymocistus* bear little resemblance to the other Aporuseae. In particular, the leaves of *Didymocistus* have more highly organized venation (fourth rank), have brachyparacytic stomata, and lack tanniniferous cells and marginal glands. The high rank and sessile, flat-topped glands suggest a possible relationship with *Hymenocardia.* Certainly the relationships of this little known, monotypic genus deserve far more consideration than Kuhlmann (1940) gave in his original description.

DRYPETEAE (GRISEB.) HURUSAWA

Drypetes Vahl. (Figs. 75–82)
See Table 4 for species examined.

Leaves microphylls to mesophylls, symmetrical, ovate, elliptic, oblong, or obovate; apex attenuate, acuminate, acute, or obtuse; base broadly acute, obtuse, or rounded, almost invariably oblique; organization of venation mid second to mid third rank; marginal ultimate ve-

TABLE 4. Species of *Drypetes* examined.

Species	Collector	Location	Herbarium
Group 1 (OTU 49)			
Sect. *Drypetes*			
alba Poit.	*Ekman 12160*	Hispanolia	DAV
diversifolia Krug & Urban	*Hackett 188*	Bahamas	UC
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
aframensis Hutch.	*Mensah FH 6732*	Ghana	GC
floribunda (Muell. Arg.) Hutch.	*Hall & Enti 40228*	Ghana	GC
natalensis (Harv.) Hutch.	*Wood (1891)*	Natal	MO
rhakodiscos (Hassk.) Airy Shaw	*Elmer 20768*	British N Borneo	UC
principum (Muell. Arg.) Hutch.	*Hall & Abbiw 44753*	Ghana	GC
Sect. unknown			
ivorensis Hutch. & Dalz.	*Hall & Abbiw 43178*	Ghana	GC
lisolinoli Leonard	*Leonard 1186*	Congo	UC
littoralis (C. B. Rob.) Merr.	*Keinholz (1924)*	Philippines	UC
Group 2 (OTU 50)			
Sect. *Drypetes*			
ilicifolia Kr. & Urb.	*Proctor 31554*	Jamaica	DAV
pellegrini Leandri	*Hall & Abbiw 44118*	Ghana	GC
perreticulata Gagnep.	*Lau 304*	China, Hainan	UC
standleyi Webster	*Foster & Croat 2308*	Panama	DAV
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
assamicus Pax & Hoffm.	*Soejarto 102*	Indonesia, cult. Hort. Bog.	DAV
aylmeri Hutch. & Dalz.	*Hall & Abbiw 44147*	Ghana	GC
battiscombei Hutch.	*Tanner 1326*	Tanganyika	UC
Sect. unknown			
gosseweileri S. Moore	*Louis 11651*	Congo	UC
iwahigensis Merr.	*Elmer 17290*	Philippines	UC
Group 3 (OTU 51)			
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
laevis (Miq.) Pax & Hoffm.	*Soejarto 95*	Indonesia, cult. Hort. Bog.	DAV
maquilingensis Merr.	*unknown*	Philippines	UC 272672
ramiflora Pax & Hoffm.	*Ramos & Edano (1928)*	Philippines	UC
Group 4 (OTU 52)			
Sect. *Oligandrae* Pax & Hoffm.			
gerrardii Hutch.	*Brass 17837*	Nyasaland	UC
lateriflora (Sw.) Kr. & Urb.	*unknown*	Mexico, Sonora	UC 44009
Sect. *Stemonodiscus* Pierre in sched.			
arguta (Muell. Arg.) Hutch.	*Schlieben 3953*	Tanganyika	MO
capillipes Pax & Hoffm.	*Louis 3479*	Congo	UC
chevalieri Beille	*Hall 43837*	Ghana	GC
gilgiana Pax & Hoffm.	*K. Da— (ill.) 215*	Gold Coast	MO
gilgiana Pax & Hoffm.	*Hall & Abbiw 43781*	Ghana	GC
leonensis Pax	*Hall & Abbiw 44732*	Ghana	GC
parvifolia (Muell. Arg.) Pax & Hoffm.	*Hall 1192*	Ghana	GC
staudtii (Pax) Hutch.	*Zenker 3398*	Cameroons	MO
Sect. *Stipulares* Pax & Hoffm.			
singroboensis Ake Assi	*Hall & Swaine 43266*	Ghana	GC

TABLE 4. Continued.

Species	Collector	Location	Herbarium
Group 5 (OTU 53)			
Sect. *Oligandrae* Pax & Hoffm.			
aubrevillei Leandri	*Hall & Swaine 43239*	Ghana	GC
Sect. *Stipulares* Pax & Hoffm.			
bipindensis (Pax) Hutch.	*Zenker 3788*	Cameroons	MO
Group 6 (OTU 54)			
Sect. *Drypetes*			
australasica Muell. Arg.	*Clemens (1944)*	Australia, Queensland	UC
deplanchei Brongn. & Gris	*McKee 1996*	New Caledonia	UC
glauca Vahl	*Webster et al. 8790*	Puerto Rico	DAV
vitiensis Croizat	*Parks 20691*	Fiji	UC

nation typically looped or fimbriate, less typically incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or rarely sclerified; stomata brachyparacytic, the subsidiary cells typically almost completely covered by the guard cells.

My observations generally agree with those of Rothdauscher (1896), Gaucher (1902), Smith and Ayensu (1964), and Hayden (1980). Smith and Ayensu, however, reported anomocytic stomata from some species. Having examined many of the same species myself, I suspect that Smith and Ayensu missed the subsidiary cells, which in many species are completely sunken beneath the guard cells and therefore difficult to see in clearings.

The teeth of *Drypetes* are traversed by a single vein that terminates below a clear, deciduous seta (Figs. 80–82), and thus are of the theoid tooth type described by Hickey and Wolfe (1975). The teeth are concave to straight along the upper side, convex along the lower side, with an obtuse apex and rounded sinus. The axis of the tooth forms an angle of about 40° to the tangent of the margin. The teeth are typically regularly distributed along the complete margin, or are absent on the apex if this is attenuate or long acuminate. In many species the teeth are little more than seta-tipped crenations (Fig. 77), whereas in a few (e.g., *D. natalense,* juvenile foliage of *D. diversifolia*) the teeth are spinose.

As the description and Table 1 indicate, leaf architecture in *Drypetes* is quite variable. Interestingly, this variation does not seem to follow Pax and Hoffmann's (1922) classification of the genus (see Table 4), which is based primarily on characters of the gynoecium and disk. Careful study of more of the approximately 160 species will be required in order to evaluate the taxonomic significance of the architectural variation.

Neowawraea Rock (OTU 90)

N. phyllanthoides Rock, U.S.A.: Hawaii, *Webster 13889* (DAV). Figures 83–85.

Leaves mesophylls, symmetrical, ovate; apex broadly acute; base rounded to subcordate; organization of venation fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

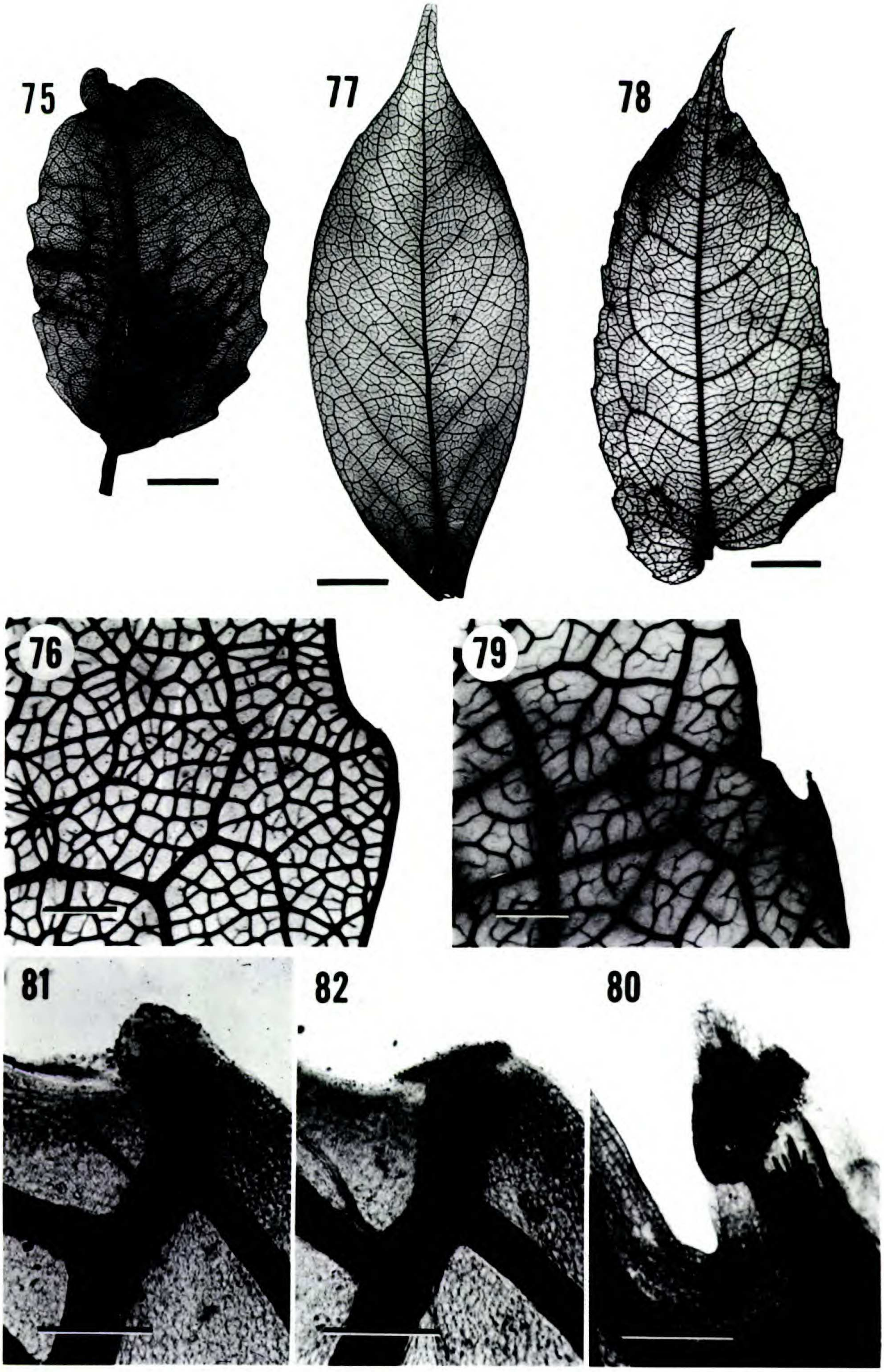
Smith and Ayensu (1964) reported that the stomata were more or less anomocytic and that crystals were absent in the specimen of *N. phyllanthoides* that they examined.

Putranjiva Wall. (OTU 55)

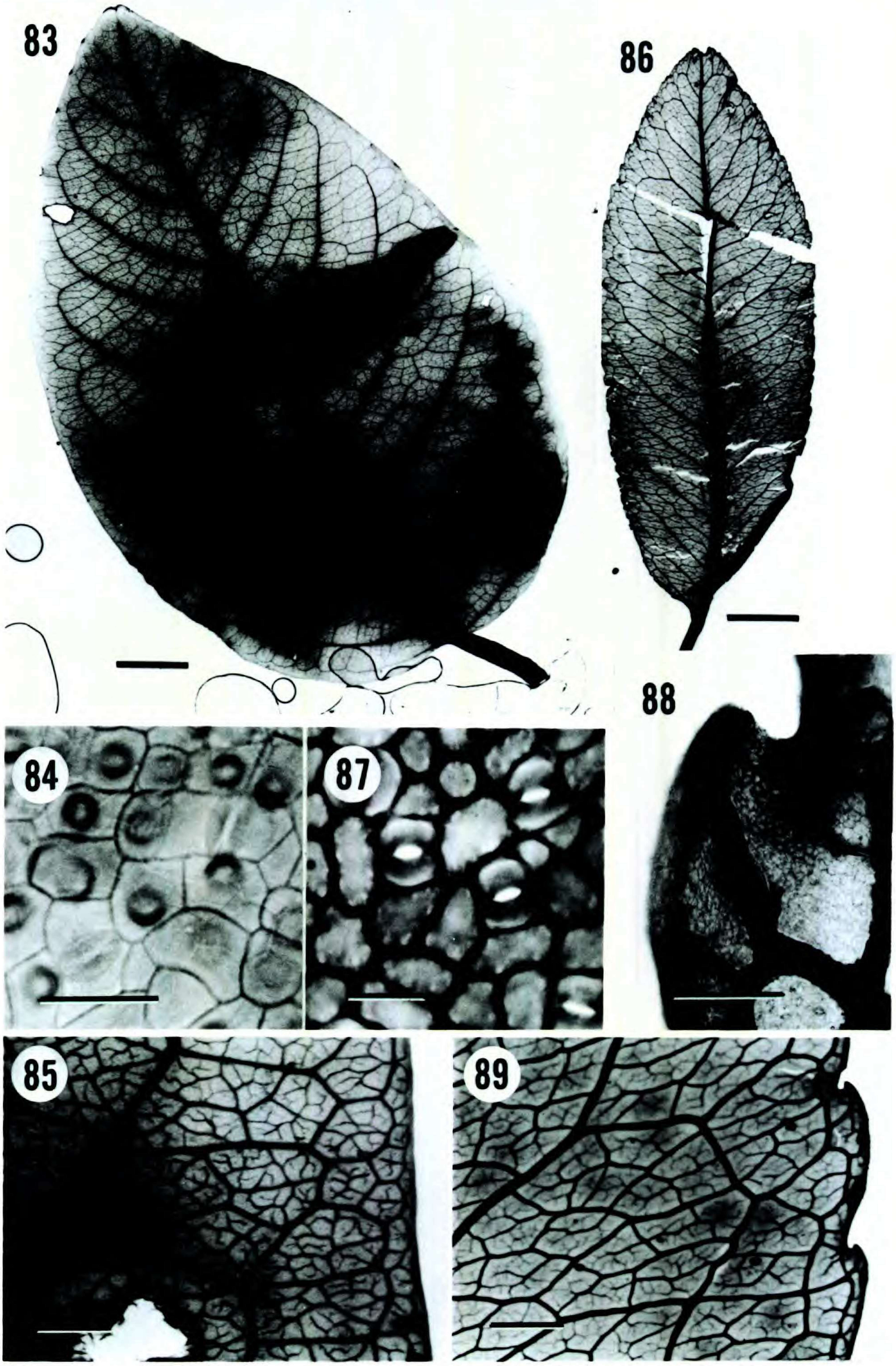
P. roxburghii Wall., Thailand: *collector illeg.* (UC 237213). Figures 86–89.

Leaves mesophylls, symmetrical, narrow elliptic; apex acute; base acute; organization of venation high second rank; marginal ultimate venation incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

The teeth of *Putranjiva,* like those of *Drypetes,* are of the theoid type. The upper side is concave to straight, the basal side convex, the apex acute, and the sinus rounded. The axis of the tooth forms an angle of about 20–25° to the tangent. The teeth are regularly distributed along the complete margin.



FIGURES 75–82. Leaves of *Drypetes.*—75, 76. *D. australasica.*—77. *D. battiscombei.*—78–80. *D. chevalieri.* The glandular seta abscises at the base of the darkly stained region.—81, 82. Teeth of *D. arguta,* with and without the deciduous seta. Bars equal 1 cm in Figures 75, 77, 78; 1 mm in Figures 76, 79; and 200 μm in Figures 80–82.



FIGURES 83–89. Leaves of *Neowawraea* and *Putranjiva*.—83–85. *Neowawraea phyllanthoides*. Note the papillae and brachyparacytic stomata in the abaxial epidermis.—86–89. *Putranjiva roxburghii*. Figure 87 shows abaxial epidermis. Bars equal 1 cm in Figures 83, 86; 1 mm in Figures 85–89; 200 μm in Figure 88; and 50 μm in Figures 84, 87.

My anatomical observations agree with Gaucher (1902).

Although Pax and Hoffmann (1922) placed *Putranjiva* in the vicinity of *Glochidion* and *Breynia* on the basis of the lack of a disk and ovary rudiment in the flowers, foliar characters support Bentham's (1880) treatment, followed by Webster (1975) and most other recent authors, in which *Putranjiva* is viewed as a close relative of *Drypetes*. Evidence from wood anatomy (Metcalfe & Chalk, 1950) and pollen morphology (Punt, 1962; Köhler, 1965) also points to this relationship. Some taxonomists, e.g., Hurusawa (1954), have even submerged *Putranjiva* in *Drypetes*. The numerous secondaries, frequent intersecondaries, and closely spaced, acute teeth that arise at a very low angle do make the leaves of *Putranjiva* distinctive, but until more is known about the architectural variation within *Drypetes*, the taxonomic significance of these characteristics cannot be determined.

Neowawraea, however, appears quite distant from *Drypetes*. Rock (1913), when he originally described the genus, likened it to *Phyllanthus*. Indeed, the wide angle of origin of the secondaries, the strongly and regularly percurrent tertiaries that form a more or less uniform oblique angle to the midrib, and the brachyparacytic stomata (Fig. 84) suggest a relationship to the more primitive genera in the Flueggeinae, such as *Margaritaria* and *Flueggea*, a relationship proposed by Stone (1967) on the basis of floral morphology. The wood, which is of the *Glochidion*-type (Hayden & Brandt, 1984), and pollen (Selling, 1947) would be more at home in this subtribe than in the Drypeteae. The putative relationship beween *Neowawraea* and *Drypetes* is particularly suspect in that *D. forbesii* Sherff, which Sherff (1939) used as the basis for reducing *Neowawraea* to synonymy with *Drypetes*, was later determined to be a previously described species of *Xylosma* in the Flacourteaceae (Sherff, 1942).

PHYLLANTHEAE DUMORT./SECURINEGINAE MUELL. ARG.

Jablonskia Webst. (OTU 56)
J. congesta (Muell. Arg.) Webst., Venezuela: Amazonas, *Ducke 1631* (UC). Figures 90, 91.

Leaves mesophylls, symmetrical, ovate to lanceolate; apex acute; base acute-cuneate; organization of venation second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or parallelocytic (with three or more lateral subsidiary cells parallel to the guard cells; Payne, 1970).

My anatomical observations agree with Rothdauscher's (1896) description of this species under its earlier name, *Securinega congesta*.

Keayodendron Leandri (OTU 57)
K. bridelioides (Mildbr.) Leandri, Gold Coast: *Vigne 3122* (A). Figure 95.

Leaves mesophylls, symmetrical, wide-elliptic; apex rounded; base obtuse-decurrent; organization of venation mid to high second rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered beneath midrib and secondaries and on margins.

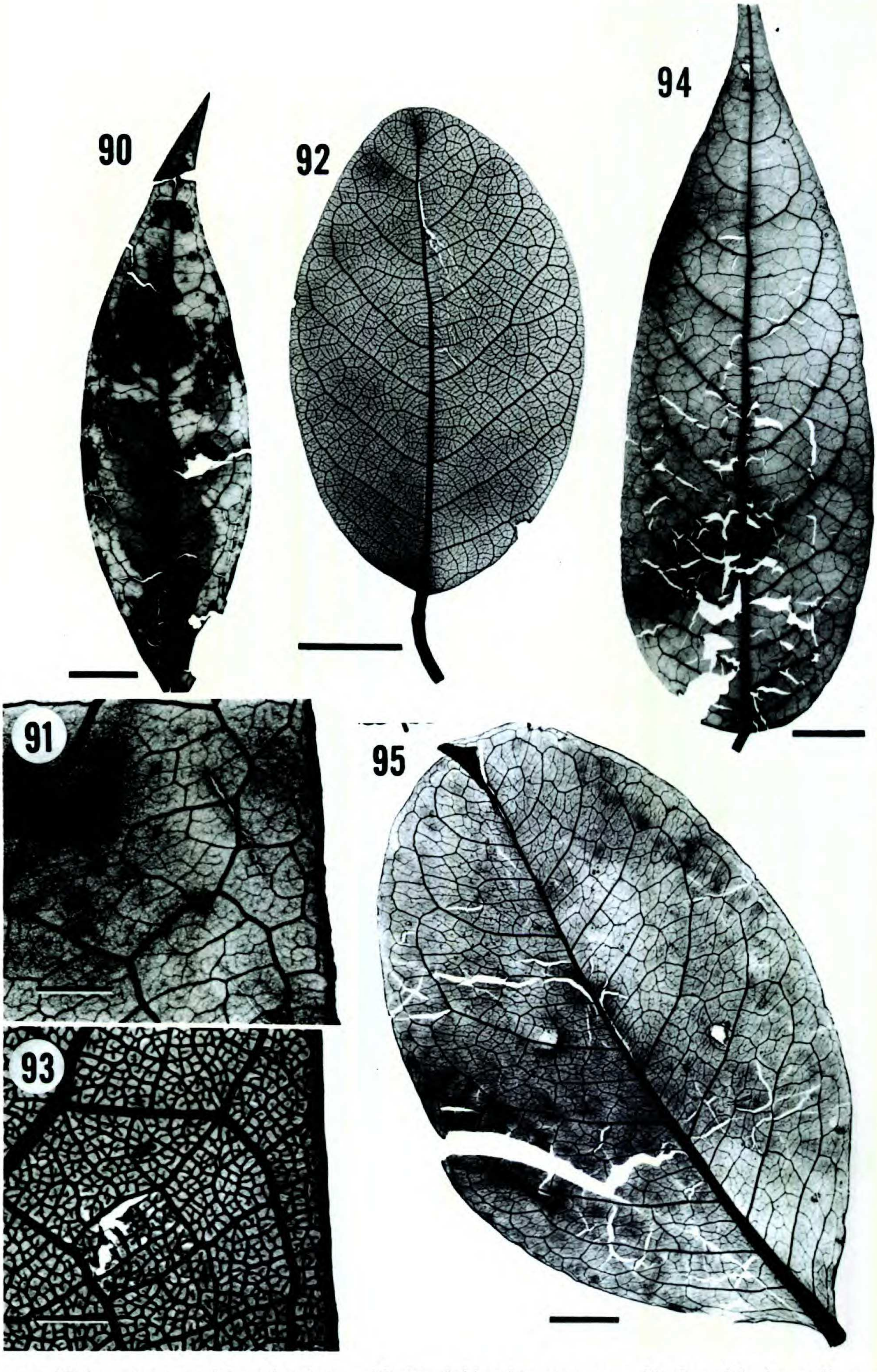
Lingelsheimia Pax (OTU 94)
L. frutescens Pax, Congo: *Leonard 1759* (UC).

Leaves mesophylls, symmetrical, elliptic; apex acuminate; base acute; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic, rarely the subsidiary cells extending beyond the guard cells at one end (Fig. 96).

Meineckia Baill. (OTU 58)
M. capillipes (Blake) Webst., Guatemala: *Pittier 384* (US).
M. neogranatensis (Muell. Arg.) Webst., Brazil: *Glaziou 13193* (DAV).
M. parvifolia (Wight) Webst., Ceylon: *Wheeler 12227* (DAV).

Leaves nanophylls to microphylls, symmetrical, elliptic or ovate; apex acute or obtuse; base acute, obtuse, or rounded; organization of venation high second to low third rank, the veins very fine; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Raju and Rao (1977) reported that the stomata of *M. parvifolia* are predominantly anisocytic. The specimens of all three species I examined possess paracytic stomata almost exclusively.



FIGURES 90–95. Leaves of Securineginae.—90, 91. *Jablonskia congesta.*—92. *Pseudolachnostylis maprounifolia.*—93. *P. glauca.*—94. *Zimmermannia acuminata.*—95. *Keayodendron bridelioides.* Bars equal 1 cm in Figures 90, 92, 94, 95 and 1 mm in Figures 91, 93.

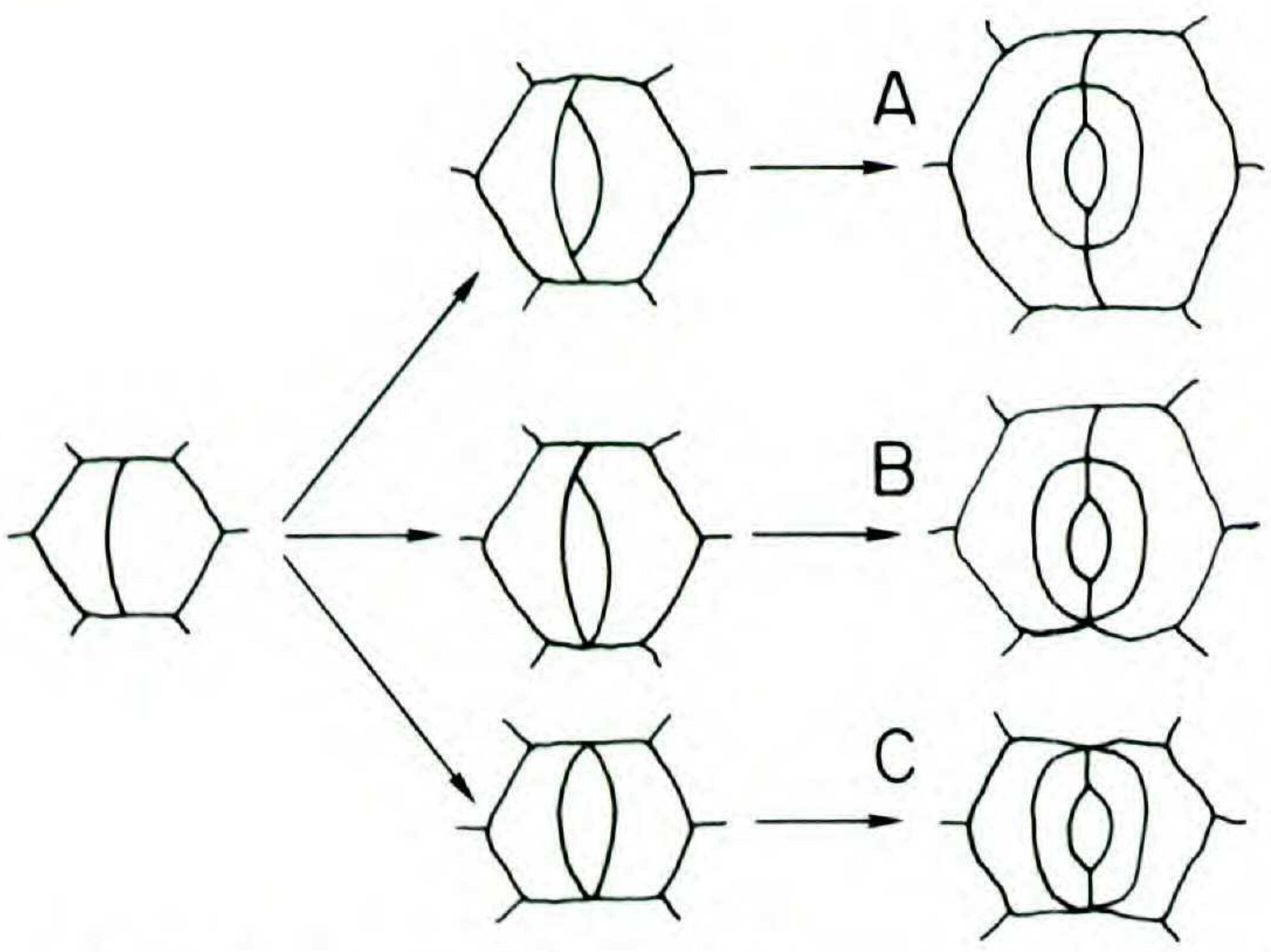


FIGURE 96. Developmental sequence typical of Flueggeinae, giving rise to paracytic (A), intermediate (B), and brachyparacytic (C) stomata. All three types appear on most leaves.

Pseudolachnostylis Pax (OTU 59)

P. dekindtii Pax, Rhodesia: *Coxe 187* (MO).
P. glauca (Hiern) Hutch., Rhodesia: *Rodin 4409* (UC). Figure 93.
P. maprouneifolia Pax, Rhodesia: *Farrell 213* (MO). Figure 92.
P. polygyna Pax & Hoffm., Rhodesia: *Stolz 1754* (CAS).

Leaves microphylls, symmetrical, elliptic or ovate; apex acute or obtuse; base obtuse to rounded or subcordate; organization of venation low fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata paracytic; trichomes typically absent, but in *P. dekindtii* dense beneath midrib and secondaries.

My observations agree with those of Gaucher (1902) and Hayden (1980).

Zimmermannia Pax (OTU 60)

Z. acuminata Verdc., Tanganyika: *Vaughn 2665* (EAH). Figure 94.
Z. capillipes Pax, Tanganyika: *Greenway 5862* (MO).

Leaves microphylls to mesophylls, symmetrical, narrow elliptic or lanceolate; apex acute or acuminate; base obtuse to rounded; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

Webster's (1975) Securineginae consist of a collection of genera not found together in any other system. Pollen evidence (Punt, 1962; Köhler, 1965) suggests two groups of genera, one consisting of *Danguyodrypetes, Lingelsheimia, Pleiostemon,* and *Zimmermannia,* and the other consisting of *Securinega* (except *S. congesta*; see below) and *Chascotheca.* Both Punt and Köhler related *Pseudolachnostylis* to *Amanoa.* The position of *Meineckia* is unclear and *Keayodendron* pollen has not been described.

Leaf morphology does little to clarify the relationships in this group, largely because the genera with aberrant pollen frequently have aberrant leaf morphology. *Lingelsheimia* and *Zimmermannia* have very similar leaves. *Pseudolachnostylis,* with its high rank leaves, is far more specialized than *Amanoa*; there is little to suggest a close relationship between the two genera. Unfortunately, the leaves of *Pseudolachnostylis* are also more specialized than the other Securineginae, although there are trends toward increasing rank in this subtribe, making *Pseudolachnostylis* more at home here than elsewhere. *Meineckia,* in contrast, exhibits lower rank, and appears most similar to *Andrachne.* This could be convergence, as both genera have herbaceous tendencies and small, thin leaves in which reversion to lower rank would be expected. Webster (1965) suggested that *Zimmermannia* is the closest relative of *Meineckia*; the leaves of the latter could easily be derived from the former by reduction in rank associated with the change in habit.

In his review of the pollen of the Euphorbiaceae, Punt (1962) pointed out that the pollen of *Securinega congesta* differed radically from the pollen of other species of *Securinega* he studied. Webster (1984b) described the new genus *Jablonskia* for this species. The leaves suggest a relationship to the Wielandieae, which also have numerous intersecondaries and random to orthogonally reticulate tertiaries. I have not examined leaves of the species that Webster maintained in *Securinega.*

FLUEGGEINAE MUELL. ARG.

Flueggea Willd. (OTU 61)

F. flexuosa Muell. Arg., Philippines: Luzon, *Elmer 15662* (UC).
F. suffruticosa (Pallas) Baillon, Hondo: *Ohwi (1951)* (UC). Figures 97, 98.
F. virosa Roxb. ex Willd., Ivory Coast: *Leeuwenberg 3317* (UC), Tanganyika: *Tanner 4266* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic; apex acute; base obtuse; organization of venation mid third rank; marginal ultimate venation incomplete or looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic or with the subsidiary cells extending beyond the guard cells at one end only (Fig. 96).

Gaucher (1902) reported sclerified bundle sheaths in *F. suffruticosa.*

I am following Webster (1984a), who recognized *Flueggea* as a genus distinct from *Securinega.*

Breynia Forst. (OTU 62)

B. acuminata Muell. Arg., Philippines: Luzon, *Clemens 16742* (UC).

B. angustifolia Hook. f., Sumatra: *Boeea 8969* (UC).

B. cernua Muell. Arg., Culion: *Herre 1024* (UC).

B. discigera Muell. Arg., Sumatra: *Yates 1171* (UC). Figure 100.

B. disticha Forst., Tuamotu Island: *Wilder 1148* (UC), Fiji: *Smith 9623* (UC). Figure 99.

B. fruticosa (L.) Hook. f., Hong Kong: *Taam 1771* (UC).

B. officinalis Hemsl., Hong Kong: *Chun 5072* (UC).

Leaves microphylls, symmetrical, ovate, elliptic, or oblong; apex acute, obtuse, or rounded; base acute, obtuse, or rounded, in many species decurrent; organization of venation high third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal or swollen (*B. acuminata, B. angustifolia, B. cernua*); bundle sheath of higher order veins parenchymatous; stomata paracytic to brachyparacytic, in many the subsidiary cells extending beyond the guard cells at one end only (Fig. 96); trichomes absent on most species, but *B. discigera* with trichomes covering abaxial epidermis (Fig. 100); epidermal cells typically papillate, in some the papillae quite elongate.

My observations of the species examined by Gaucher (1902), Raju and Rao (1977), and Hayden (1980) agree with their reports.

Glochidion Forst.

See Table 5 for species examined. (Figs. 101, 102)

Leaves microphylls or small mesophylls, symmetrical or asymmetrical (sect. *Hemiglochidion* pro parte), ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate, oblique in species with asymmetrical blades; organization of venation high third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or sclerified; stomata brachyparacytic, in some the subsidiary cells extending beyond the guard cells at one end (Fig. 96); trichomes sparse to dense on abaxial epidermis, particularly dense beneath veins, in some species also on adaxial epidermis, or the leaves glabrous.

My anatomical observations do not conflict with those of Gaucher (1902).

Three groups of species can be recognized on the basis of leaf architecture. Section *Glochidion* (OTU 63) has symmetrical leaves with tertiaries that are predominantly perpendicular to the midrib. Section *Hemiglochidion* can be divided into two groups, the first (OTU 64) with symmetrical leaves and tertiaries that vary from oblique to perpendicular to the midrib with the angle decreasing upwards in the leaf, and the second (OTU 65) with asymmetrical leaves with oblique bases and tertiaries that are predominantly perpendicular to the midrib.

Margaritaria L. f. (OTU 67)

M. nobilis L., Panama: *Luteyn & Foster 949* (G). Figures 103, 104.

M. obovata (Baill.) Webst., Tanganyika: *Tanner 3774* (UC).

M. scandens (Wr. ex Griseb.) Webst., Bahamas: Andros, *Brace 4867* (NY).

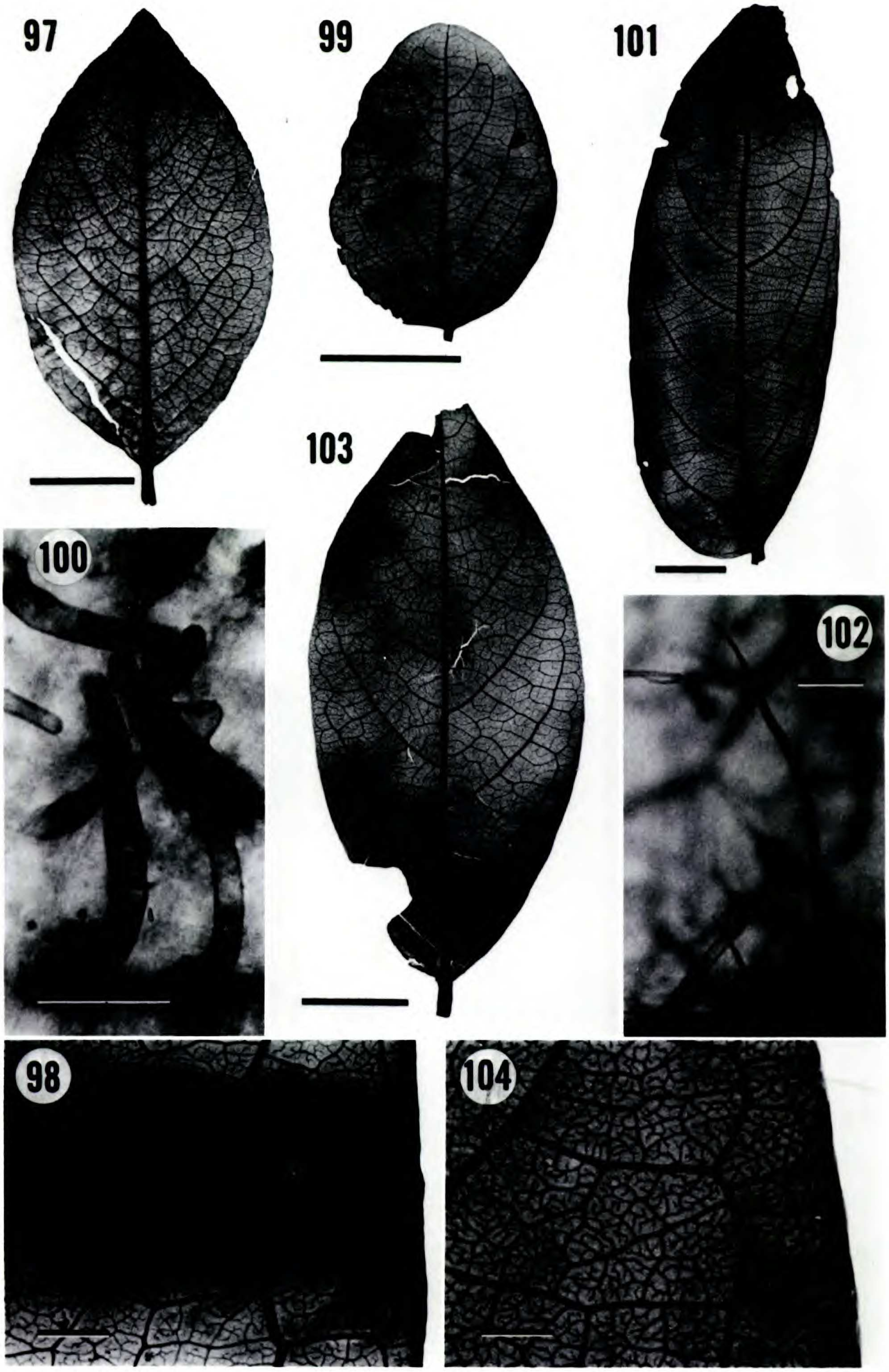
M. tetracocca (Baill.) Webst., Cuba: *Leon & Clemente 23339* (NY).

Leaves microphylls, symmetrical, obovate or elliptic; apex acute, obtuse, or rounded; base acute, obtuse, or rounded; organization of venation mid third rank; marginal ultimate venation looped or fimbrate; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata brachyparacytic; trichomes none or scattered beneath veins.

Phyllanthus L.

See Table 6 for species examined.

Leaves nanophylls, microphylls, or mesophylls, symmetrical or some asymmetrical, ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate, some oblique; organization of venation low second to mid third rank; marginal ultimate venation incomplete or looped; terminal tracheids normal or swollen; bundle sheath of higher



FIGURES 97–104. Leaves of Flueggeinae.—97, 98. *Flueggea suffruticosa*.—99. *Breynia disticha*.—100. Multicellular trichomes of *B. discigera*.—101. *Glochidion philippicum*.—102. Multicellular trichomes of *G. eriocarpum*.—103, 104. *Margaritaria nobilis*. Bars equal 1 cm in Figures 97, 99, 101, 103; 1 mm in Figures 98, 104; and 100 μm in Figures 100, 102.

TABLE 5. Species of *Glochidion* examined.

Species	Collector	Location	Herbarium
Group 1 (OTU 63)			
Sect. *Glochidion*			
atalotrichum A. C. Smith	*Smith 8747*	Fiji	UC
cordatum (Muell. Arg.) Seem.	*Smith 9403*	Fiji	UC
dasyphyllum K. Koch	*Merrill 10810*	China, Kwangtung	UC
dasyphyllum K. Koch	*Chun 6405*	China, Kwangtung	UC
eriocarpum Champ.	*Lei 899*	China, Hainan	UC
hirsutum Wight	*Boeea 6700*	Sumatra	UC
hongkongense Muell. Arg.	*Chun 4783*	China, Lantoa Island	UC
lancifolium C. B. Rob.	*Ramos & Edano (1924)*	Philippines	UC
littorale Bl.	*Clemens (1915)*	British N Borneo	UC
Group 2 (OTU 64)			
Sect. *Hemiglochidion* Muell. Arg.			
daltoni Kurcz	*Maire 3865*	China, Yunnan	UC
ferdinandi Muell. Arg.	*White (1926)*	Australia, Queensland	UC
fortunei Hance	*Merrill 11369*	China, Kaingsu	UC
merrillii C. B. Rob.	*Clemens 18750*	Philippines	UC
obovatum Sieb. & Zucc.	*Hiroe 14033*	Japan	UC
rubrum Bl.	*Skukor AS 95*	Malaya	UC
seemannii Muell. Arg.	*Smith 8758*	Fiji	UC
Group 3 (OTU 65)			
album (Blco.) Boerl.	*Ramos & Edano (1927)*	Philippines	UC
benguetense Elm.	*Ramos & Edano (1926)*	Philippines	UC
borneense Boerl.	*Yates 2481*	Sumatra	UC
bracteatum Gill.	*Smith 7366*	Fiji	UC
fagifolium Miq.	*Liang 62257*	China, Hainan	UC
hypoleucum (Miq.) Boerl.	*Cenabre (1924)*	Philippines	UC
lanceolatum Hay	*Chuang & Kao 5541*	Taiwan	UC
leiostylum Kurz.	*Toroes 3834*	Sumatra	UC
philippicum (Cav.) C. B. Rob.	*Ramos (1925)*	Philippines	UC
puberum (D.) Hutch.	*Gressitt 1407*	China, Kwangtung	UC
wrightii Benth.	*Gressitt 1111*	China, Hainan	UC

order veins parenchymatous or sclerified; stomata brachyparacytic or the subsidiary cells extending beyond the guard cells at one end (Fig. 96); trichomes present beneath veins or covering the abaxial epidermis, or none; abaxial epidermis typically papillate, the papillae quite long in many species.

The leaves of most *Phyllanthus* species are borne on determinate plagiotropic branches that mimic compound leaves, a condition termed phyllanthoid branching (Webster, 1956, 1967). As the description and Table 1 indicate, these leaves vary considerably, the diversity within this one huge genus equalling or exceeding the entire subfamily. Many more of the 600–700 species must be examined before any evaluation of the overall taxonomic value of the foliar morphology can be made. Early steps in this direction were made by Webster (1956, 1957, 1958) in his monograph of the West Indian species, but far more remains to be done.

Reverchonia A. Gray

R. arenaria A. Gray, U.S.A.: Texas, *Rowell 11531* (DAV). Figure 105.

Leaves nanophylls, symmetrical, narrow-elliptic to oblanceolate; apex obtuse; base acute; margin entire; organization of venation high first rank; venation pinnate, brochidodromous, all the vein orders beyond the primary very fine; primary vein massive, straight; secondary veins

TABLE 6. Species of *Phyllanthus* examined.

Species	Collector	Location	Herbarium
Sect. *Adenoglochidion* Muell. Arg. (OTU 68)			
aeneus Baill.	*Baumann 6295*	New Caledonia	DAV
aeneus Baill.	*Baumann 6286*	New Caledonia	DAV
Sect. *Anisonema* (A. Juss.) Griseb. (OTU 69)			
microcarpus (Benth.) Muell. Arg.	*Bartlett 14708*	Philippines	UC
reticulatus Poir.	*Tanner 3720*	Tanganyika	UC
Sect. *Aporosella* (Chodat) Webster (OTU 70)			
chacoensis Morong.	*Eyerdam & Beetle 22983*	Argentina	UC
Sect. *Cicca* (L.) Muell. Arg. (OTU 71)			
acidus (L.) Skeels	*Mexia 1005*	Nayarit	UC
acidus (L.) Skeels	*Berngardt (1923)*	Philippines (cult.)	UC
distichus H. & A.	*Webster 1631*	Hawaii	UC
Sect. *Eleutherogynium* Muell. Arg. (OTU 72)			
induratus S. Moore	*Baumann 12504*	New Caledonia	DAV
loranthoides Baill.	*Webster 14780*	New Caledonia	DAV
Sect. *Emblica* (Gartn.) Baill. (OTU 73)			
emblica L.	*Lei 446*	China, Hainan	UC
Sect. *Floribundi* Pax & Hoffm. (OTU 74)			
floribundus Muell. Arg.	*Tanner 3022*	Tanganyika	UC
Subg. *Gomphidium* Baill.			
Group 1 (OTU 75)			
comptonii (S. Moore) Guill.	*Guillaumin 9520*	New Caledonia	US
comptonii (S. Moore) Guill.	*Webster 14829*	New Caledonia	DAV
ripicolus Guill.	*Guillaumin 7232*	New Caledonia	A
Group 2 (OTU 76)			
balanseanus Guill.	*Webster 14735*	New Caledonia	DAV
bourgeosii Baill.	*Guillaumin & Baumann 7547*	New Caledonia	DAV
buxoides Guill.	*McMillan 5103*	New Caledonia	UC
cornutus Baill.	*Baumann 13486*	New Caledonia	DAV
pancherianus Baill.	*Guillaumin & Baumann 6577*	New Caledonia	DAV
poumensis Guill.	*Webster 14642*	New Caledonia	DAV
poumensis Guill.	*McKee 4620*	New Caledonia	UC
Sect. *Hemicicca* (Baill.) Muell. Arg. (OTU 77)			
flexuosus (Sieb. & Zucc.) Muell. Arg.	*Kasapligil 3640*	China, Honshu	UC
Sect. *Heteroglochidion* Muell. Arg. (OTU 78)			
baladensis Baill.	*Webster 14875*	New Caledonia	DAV
francii Guill.	*Guillaumin 8408*	New Caledonia	DAV
peltatus Guill.	*Webster 14645*	New Caledonia	DAV
pronyensis Guill.	*Webster 14414*	New Caledonia	DAV
salacioides S. Moore	*Webster 14871*	New Caledonia	DAV
serpentinus S. Moore	*McKee 4568*	New Caledonia	UC
Sect. *Nothoclema* Webster (OTU 79)			
acuminatus Vahl.	*Dwyer & Duke 7916*	Panama	UC
acuminatus Vahl.	*Hinton et al. 15965*	Mexico	UC

TABLE 6. Continued.

Species	Collector	Location	Herbarium
Sect. *Nymphanthus* (Lour.) Muell. Arg. (OTU 80)			
ruber (Lour.) Spreng.	*Gressitt s.n.*	China, Hainan	UC 1352893
Sect. *Paragomphidium* Muell. Arg. (OTU 81)			
vieillardii Baill.	*Webster 14711*	New Caledonia	DAV
Sect. *Phyllanthodendron* (Hemsl.) Beille (OTU 82)			
mirabilis Muell. Arg.	*Wolfe (1964)*	England, cult. Kew	—
Sect. *Polyandroglochidion* S. Moore (OTU 83)			
ngoyensis Schltr.	*McMillan 5184*	New Caledonia	UC
Sect. *Psychoglochidion* Muell. Arg. (OTU 84)			
koghiensis Guill.	*Webster 14589*	New Caledonia	DAV
Sect. *Scepasma* (Bl.) Muell. Arg. (OTU 85)			
buxifolius (Bl.) Muell. Arg.	*Ramos (1923)*	Philippines	UC

arising acutely at a more or less uniform angle of about 50°, course curved abruptly, loops joining at an obtuse angle; tertiary veins originating at random angles, transverse ramified; highest vein order tertiary; marginal ultimate venation incomplete; areoles extremely irregular in size and shape; veinlets branched once or twice; terminal tracheids swollen; bundle sheath of all veins parenchymatous; epidermal cells isodiametric; arranged randomly, with straight anticlinal walls; stomata equally abundant on both epidermises (stomatal frequency about 12%), with anomocytic stomata; trichomes and crystals absent.

My observations agree with Hayden (1980).

Richeriella Pax & Hoffm. (OTU 86)

R. gracilis (Merr.) Pax & Hoffm., China: Hainan, *Liang 65438* (UC).

Leaves microphylls, symmetrical, elliptic; apex acuminate; base obtuse; organization of venation mid second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

Sauropus Bl. (OTU 87)

S. androgynus (L.) Merr., Malaya: *Yapp 198* (UC).

S. grandifolius Pax & Hoffm., Cochinchina: *Pierre s.n.* (UC).

S. hirsutus Beille, Cochinchina: *Pierre 564* (UC).

S. rhamnoides Bl., British N Borneo: *Elmer 20803* (UC).

S. spectabilis Miq., Indonesia: *cult. Hort. Bog.* (UC 301610).

Leaves microphylls to mesophylls, symmetrical, lanceolate, ovate, or elliptic; apex acuminate, acute, or obtuse; base obtuse; organization of venation mid to high third rank; marginal ultimate venation incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic to paracytic, the subsidiary cells extending beyond the guard cells at one end only (Fig. 96).

My anatomical observations on these five species agree with Rothdauscher (1896), who studied four others.

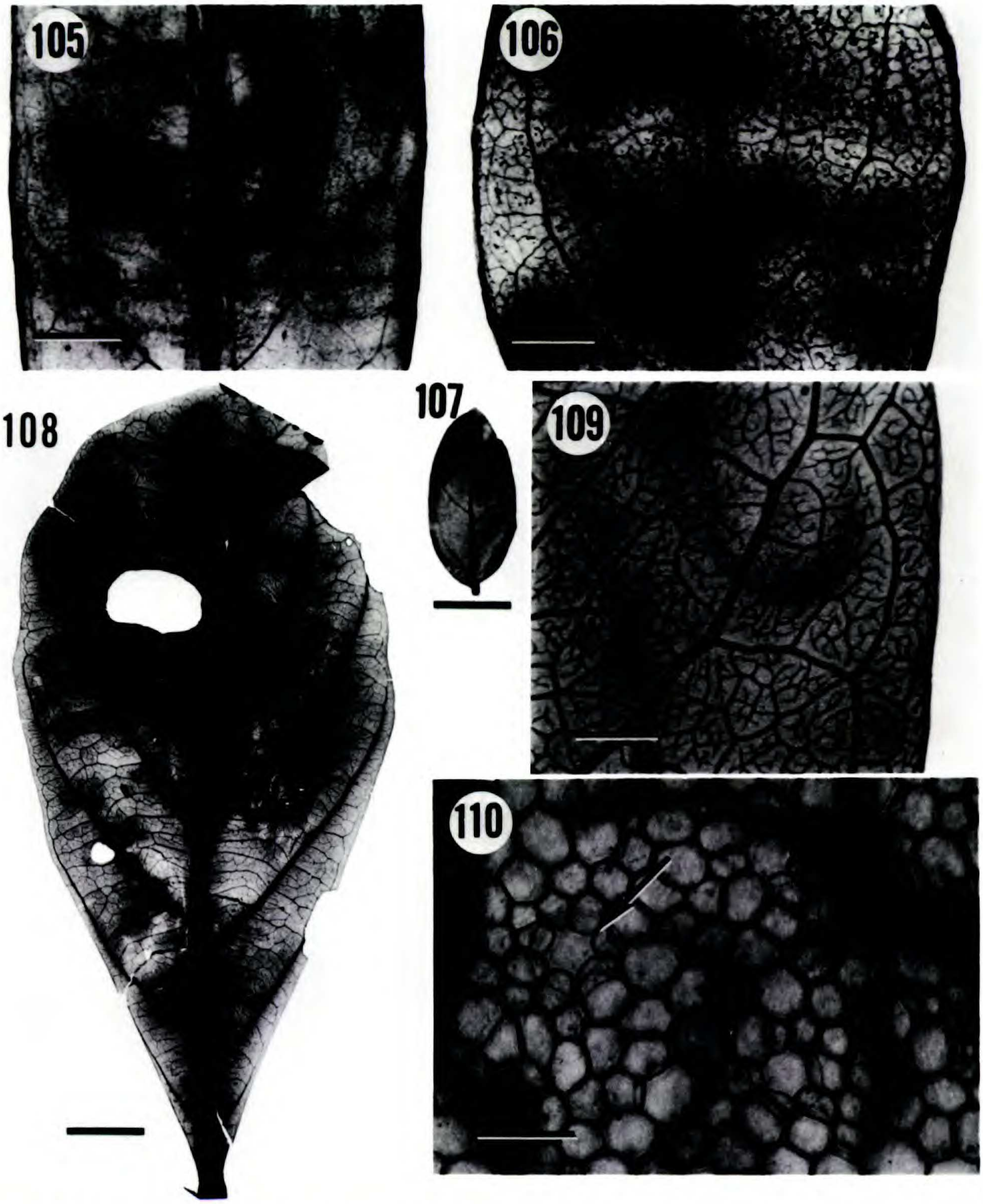
Synostemon F. Muell. (OTU 66)

S. bacciforme (L.) Webst., Ceylon: *Wheeler 12034* (DAV). Figures 106, 107.

S. thesioides Hj. Eichl., Australia: South Australia, *Lothian 3234* (UC).

Leaves nanophylls, symmetrical, obovate; apex rounded, mucronate; base obtuse to rounded; organization of venation first rank; marginal ultimate venation incomplete; terminal tracheids normal (*S. thesioides*) or swollen (*S. bacciforme*); bundle sheath of higher order veins parenchymatous; stomata brachyparacytic or the subsidiary cells extending beyond the guard cells at one end only (Fig. 96); epidermis of *S. thesioides* containing groups of sclerified, papillate cells.

My observations of the epidermis of *S. bacciforme* agree with those of Raju and Rao (1977).



FIGURES 105–110. Leaves of *Reverchonia, Synostemon,* and *Uapaca.*—105. *Reverchonia arenaria.*—106, 107. *Synostemon bacciforme.*—108. *Uapaca guineensis.*—109. *U. heudelotii.*—110. Adaxial epidermis of *U. nitida,* with tanniniferous epidermal cells (arrow). Bars equal 1 cm in Figure 108; 5 cm in Figure 107; 1 mm in Figures 105, 106, 109; and 100 μm in Figure 110.

In contrast to the Securineginae, the Flueggeinae appear to form a closely knit group. *Flueggea, Margaritaria,* and *Richeriella,* the more primitive genera in the subtribe, have very similar leaf architecture and epidermal morphology. The more primitive sections of *Phyllanthus* that I examined, e.g., *Anisonema, Cicca,* and *Floribundi,* share many features with these three genera.

Apparently the shift within *Phyllanthus* to phyllanthoid branching (Webster, 1956, 1967), in which determinate, plagiotropic lateral branchlets mimic pinnate leaves, has led to an adaptive radiation into a variety of habitats with an attendant radiation in foliar morphology. The leaf architectural diversity within *Phyllanthus* and its closely related segregates, *Breynia, Glochidion, Sauropus, Synostemon,* and (probably) *Rev-*

erchonia (Webster, 1967; Webster & Miller, 1963) equals that of the rest of the subfamily, reflecting this radiation. Still, certain patterns can be detected. All these genera, with the exception of the herbaceous *Reverchonia*, share a similar stomatal development pattern, in which the divisions giving rise to the subsidiary cells and the guard mother cell exhibit a certain flexibility, giving rise to paracytic, brachyparacytic, and intermediate stomata on the same leaf (Fig. 96). As Webster (1956, 1957, 1958) and Raju and Rao (1977) demonstrated, the herbaceous taxa within this plexus, which are not closely related to each other, generally bear aniso- or anomocytic stomata, suggesting that the latter pattern in *Reverchonia* results from convergence. Also, the similarity of *Breynia, Glochidion,* and *Sauropus* suggests that they may belong to a single line derived from the more central *Phyllanthus* subgenera. The taxonomist interested in studying this group in detail should find leaf morphology a rich source of information.

HYMENOCARDIEAE (MUELL. ARG.) HUTCH.

Hymenocardia Wall. ex Lindl. (OTU 89)

H. acida Tul., Ghana: *Enti R775* (RSA).

H. laotica Gagnep., Indochina: *Thorel 1989* (UC).

H. lyrata Tul., Ivory Coast: *Leeuwenberg 2987* (UC).

H. mollis Pax, Tanganyika: *Tanner 5258* (UC). Figure 111.

H. wallichii Tul., Burma: *Dickason 6879* (RSA). Figure 112.

Leaves microphylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, or obtuse; base acute, obtuse, or rounded; organization of venation low fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; unicellular trichomes typically above and beneath midrib and secondaries, in some species also beneath other veins, abaxially in junctions of midrib and secondaries, scattered on abaxial epidermis, or none; sessile, disk-shaped glands somewhat sunken in pits on the abaxial epidermis.

My anatomical observations agree with those of Rothdauscher (1896), Gaucher (1902), and Pax and Hoffmann (1922).

The leaf morphology of *Hymenocardia* reveals little about its relationships within the Phyllanthoideae, although the high rank of the leaves suggests proximity to the Phyllantheae. This is in accord with its wood, which is of the *Glochidion* type (Metcalfe & Chalk, 1950). Only *Didymocistus* bears similar sunken disk-shaped glands, suggesting that these genera are related.

Airy Shaw (1965) recognized for *Hymenocardia* a distinct family related to the Ulmaceae on the basis of the winged fruits and pollen that closely resembles *Celtis*. The leaves of *Hymenocardia* are of much lower rank than is typical of the Ulmaceae and have symmetrical bases in contrast to *Celtis* and many other members of the Ulmaceae. Nothing in its foliar morphology suggests that *Hymenocardia* is out of place in the Euphorbiaceae, and both wood anatomy (Metcalfe & Chalk, 1950) and chromosome numbers (Mangenot & Mangenot, 1958; Webster & Ellis, 1962) support its retention.

UAPACEAE (MUELL. ARG.) HUTCH.

Uapaca Baill. (OTU 88)

U. guineensis Muell. Arg., Nigeria: *Ujor FHI 26153* (DAV), Liberia: *Voorhoeve 771* (UC). Figure 108.

U. heudelotii Baill., Nigeria: *Taylor FHI 31132* (DAV), Cameroons: *Bereteler et al. 2541* (UC), *Zenker 59* (UC). Figure 109.

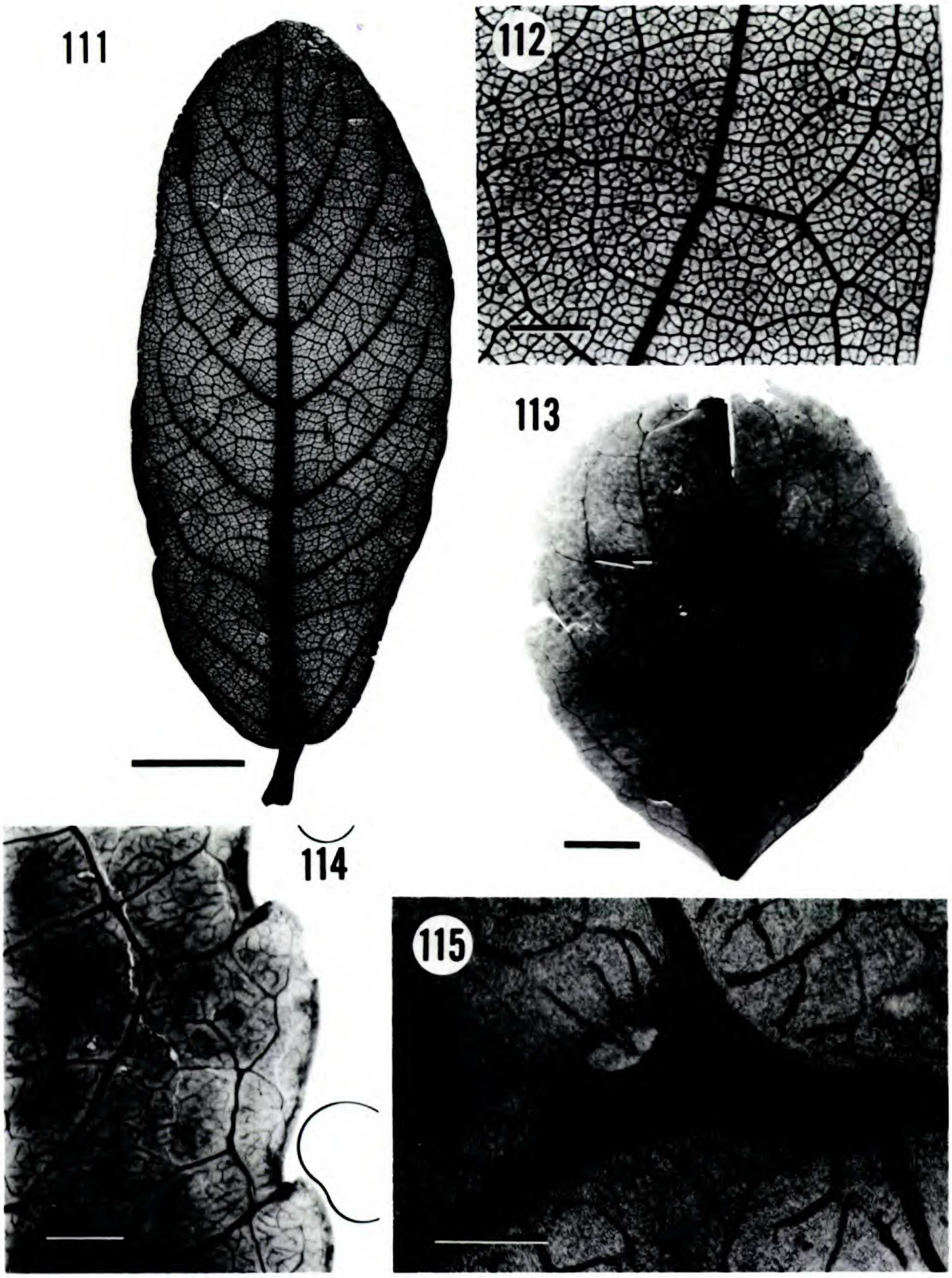
U. nitida Muell. Arg., Rhodesia: *Rodin 4397* (UC). Figure 110.

U. sansibarica Pax, Nyasaland: *Brass 17466* (UC).

U. togoensis Pax, Nigeria: *Onochie FHI 32206* (DAV).

Leaves microphylls to mesophylls, symmetrical, obovate to oblanceolate; apex obtuse to rounded; base acute-cuneate; organization of venation mid third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes beneath veins (*U. sansibarica, U. togoensis*) or none; elongate tanniniferous cells originating in the epidermis and running through the mesophyll; tanniniferous cells in epidermis.

My anatomical observations generally agree with those of Gaucher (1902) and Comyn (1947), except that neither of them reported the large spherical tanniniferous cells in the epidermis. Comyn's (1947) illustrations of stomata from several species show the guard cells surrounded by a single subsidiary cell, a pattern that is known only from a few ferns (Fryns-Claessens & van Cotthem, 1973).



FIGURES 111–115. Leaves of *Hymenocardia* and *Bischofia*.—111, 112. *Hymenocardia mollis*.—113, 114. Terminal leaflet of *Bischofia javanica*. Arrow indicates position of one domatium.—115. Marsupiform domatium of *B. javanica*. Bars equal 1 cm in Figures 111, 113; 1 mm in Figures 112, 114; and 500 μm in Figure 115.

The leaf morphology of *Uapaca* is particlarly intriguing because the genus has unique involucrate heads of disk-less flowers and its affinities thus cannot be determined using traditional characters. Architecturally *Uapaca* appears most like the Antidesmeae/Aporuseae; the large tanniniferous epidermal cells and anisocytic stomata strongly suggest a relationship to the Aporuseae. Pollen (Punt, 1962; Köhler, 1965) and wood anatomy (Metcalfe & Chalk, 1950) contribute little toward resolving the question.

Airy Shaw's (1965) suggestion of an affinity between *Uapaca* and the Anacardiaceae gains no support from foliar morphology. Anacardiaceae leaves typically are pinnately compound and exhibit distinct tendencies for the secondary veins to thin markedly at the margin and for the tertiary veins to thin markedly between the secondaries (J. Wolfe, pers. comm.). *Uapaca* shares none of these characteristics and also has higher venation that branches less than is typical of the Anacardiaceae (pers. observ.). Furthermore, Anacardiaceae generally have anomocytic stomata (Metcalfe & Chalk, 1950).

BISCHOFIEAE (MUELL. ARG.) HURUSAWA

Bischofia Bl. (OTU 91)

B. javanica Bl., Philippines: Mindanao, *Elmer 13895* (UC), Luzon: *Elmer 15228* (UC), U.S.A.: cult. California, *Reid s.n.* (DAV 88589). Figures 113–118.

Leaves trifoliolate, mesophylls; leaflets symmetrical above the base, obovate; apex obtuse to rounded; base obtuse, symmetrical on terminal leaflet, asymmetrical on lateral leaflets; organization of venation second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; marsupiform domatia abaxially in junctions of midrib and secondaries and secondaries and tertiaries; irregularly shaped secretory cells in epidermis.

My observations agree with those of Rothdauscher (1896), Gaucher (1902), Penzig and Chiabrera (1903), and Raju and Rao (1977).

The teeth of *Bischofia* are traversed by a single vein that is shifted toward the sinus and ends with a flared tip below a clear, flame-shaped, deciduous glandular seta, also shifted toward the sinus (Figs. 114, 116–118). They are thus best interpreted as modified theoid teeth (Hickey & Wolfe, 1975). The teeth are concave on the upper side, convex on the lower side, with a rounded apex and rounded sinus. The axis of the tooth forms an angle of about 15° to the tangent. The teeth are regularly distributed along the upper two-thirds of the margin.

Within the Phyllanthoideae, the compound leaves and marsupiform domatia of *Bischofia* are unique. Airy Shaw (1967) pointed out that the terminal petiolule is longer than the lateral ones, suggesting that the leaf is basically pinnately rather than palmately compound, having become trifoliolate through loss of leaflets. In further support of his hypothesis, he cited a specimen bearing a pinnately 5-foliolate leaf and previous reports of young shoots with 5-foliolate leaves. Other genera of the Euphorbiaceae have compound leaves, but these are apparently palmate. This evidence would seem to support his earlier proposal of the family Bischofiaceae, to be near the Staphyleaceae because of supposed similarity in habit and foliage between *Bischofia* and *Tapiscia* (Airy Shaw, 1965).

The bulk of the evidence suggests otherwise. The floral morphology of *Bischofia* and the Staphyleaceae is completely different (Webster, 1967), as is the wood anatomy (W. J. Hayden, pers. comm.). Significantly, *Bischofia* has pendent, anatropous, bitegmic, crassinucellate ovules, with the micropyle roofed by a placental obturator (Bhatnagar & Kapil, 1974), a suite of characteristics that is diagnostic of the Euphorbiaceae (Webster, 1967) and not found in the Staphyleaceae (Davis, 1966). Foliar similarity is only superficial. Rather than theoid teeth, *Tapiscia* and other staphyleaceous genera have cunonioid teeth, in which the vein leading into the tooth forks, with one branch ending in a knot in the sinus and the other continuing into the tooth (Hickey & Wolfe, 1975 and pers. observ.). Further, in *Tapiscia* leaves, the venational organization is of higher rank than in the *Bischofia,* and the former have semicraspedodromous venation and anisocytic stomata (pers. observ.).

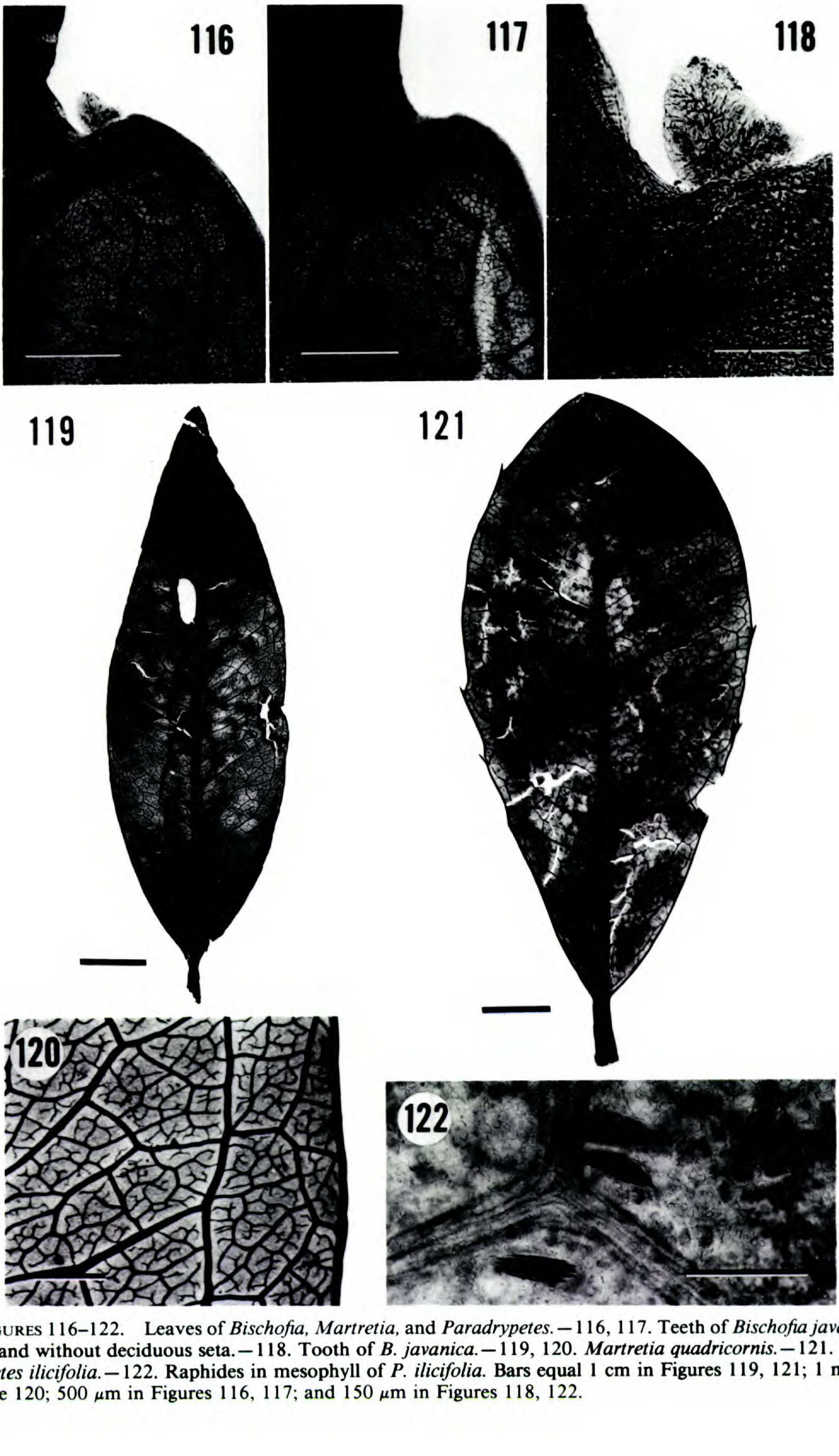
Based on this evidence, *Bischofia* is probably best placed in a separate tribe in the Phyllanthoideae, as originally proposed by Hurusawa (1954) and accepted by Webster (1975). Both phenetic and cladistic analyses of leaf characters emphasize the isolation of *Bischofia* (Levin, 1986 and in press).

GENERA OFTEN INCLUDED IN THE EUPHORBIACEAE BUT EXCLUDED BY WEBSTER (1975)

Martretia Beille (OTU 92)

M. quadricornis Beille, Congo: *Corbisier-Boland 1391* (MO), Ivory Coast: *Leeuwenberg 2697* (UC). Figures 119, 120.

Leaves large microphylls or small mesophylls, symmetrical, narrow elliptic; apex acute; base acute; organization of venation mid second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.



FIGURES 116–122. Leaves of *Bischofia, Martretia,* and *Paradrypetes.*—116, 117. Teeth of *Bischofia javanica,* with and without deciduous seta.—118. Tooth of *B. javanica.*—119, 120. *Martretia quadricornis.*—121. *Paradrypetes ilicifolia.*—122. Raphides in mesophyll of *P. ilicifolia.* Bars equal 1 cm in Figures 119, 121; 1 mm in Figure 120; 500 μm in Figures 116, 117; and 150 μm in Figures 118, 122.

The foliar morphology of *Martretia* fits well within the Phyllanthoideae, and is most similar to *Actephila* (Levin, 1986 and in press), which share the straight-sided intercostal areas with frequent intersecondaries and reticulate tertiaries. However, the false partition in the fruit (Pax & Hoffmann, 1922) and atriate apertures in the pollen (Punt, 1962; Köhler, 1965) would be unique within the Phyllanthoideae. Clearly more information on this monotypic genus is required before its relationships will be understood.

Paradrypetes Kuhlm.
P. ilicifolia Kuhlm., Brazil: Tombos, *Barreto 1663* (F). Figures 121–123.

Leaves simple, mesophylls, symmetrical, obovate; apex obtuse; base acute; margin with spinose teeth; organization of venation low third rank, pinnate, weakly brochidodromous; primary vein stout, straight; secondary veins arising at a wide acute angle, the angle more or less uniform, their thickness moderate, course curved abruptly, loop-forming branches joining acutely and accompanied by uniform tertiary loops; intersecondary veins composite, zig-zag, one present in each intercostal area and running its length; tertiaries originating from secondaries at acute angles, weakly percurrent, branching to form intersecondaries, essentially parallel to the midrib; fourth order veins orthogonal, their size moderate; fifth and sixth order veins random, their sizes moderate; highest vein order sixth; marginal ultimate venation fimbriate; areole development imperfect, arrangement random, shape triangular to polygonal, size moderate; veinlets simple or branched once; terminal tracheids normal; bundle sheath of higher order veins sclerified; epidermal cells isodiametric, arrangement random, anticlinal walls curved; stomata abaxial, orientation random, stomatal index about 12%, basically paracytic, but each subsidiary cell divided again by one or more wall at right angles to the guard cells, thus similar to the laterocytic type of den Hartog and Baas (1978); trichomes none; crystals present as raphides in abundant idioblasts just below the epidermis.

The teeth of *Paradrypetes* are spinose, traversed by a single vein terminating in a point at the tooth apex. Both sides of the tooth are straight, the apex acute, and the sinus rounded. The axis of the tooth forms an angle of about 25° to the tangent. The teeth are distributed very irregularly along the upper two-thirds of the margin.

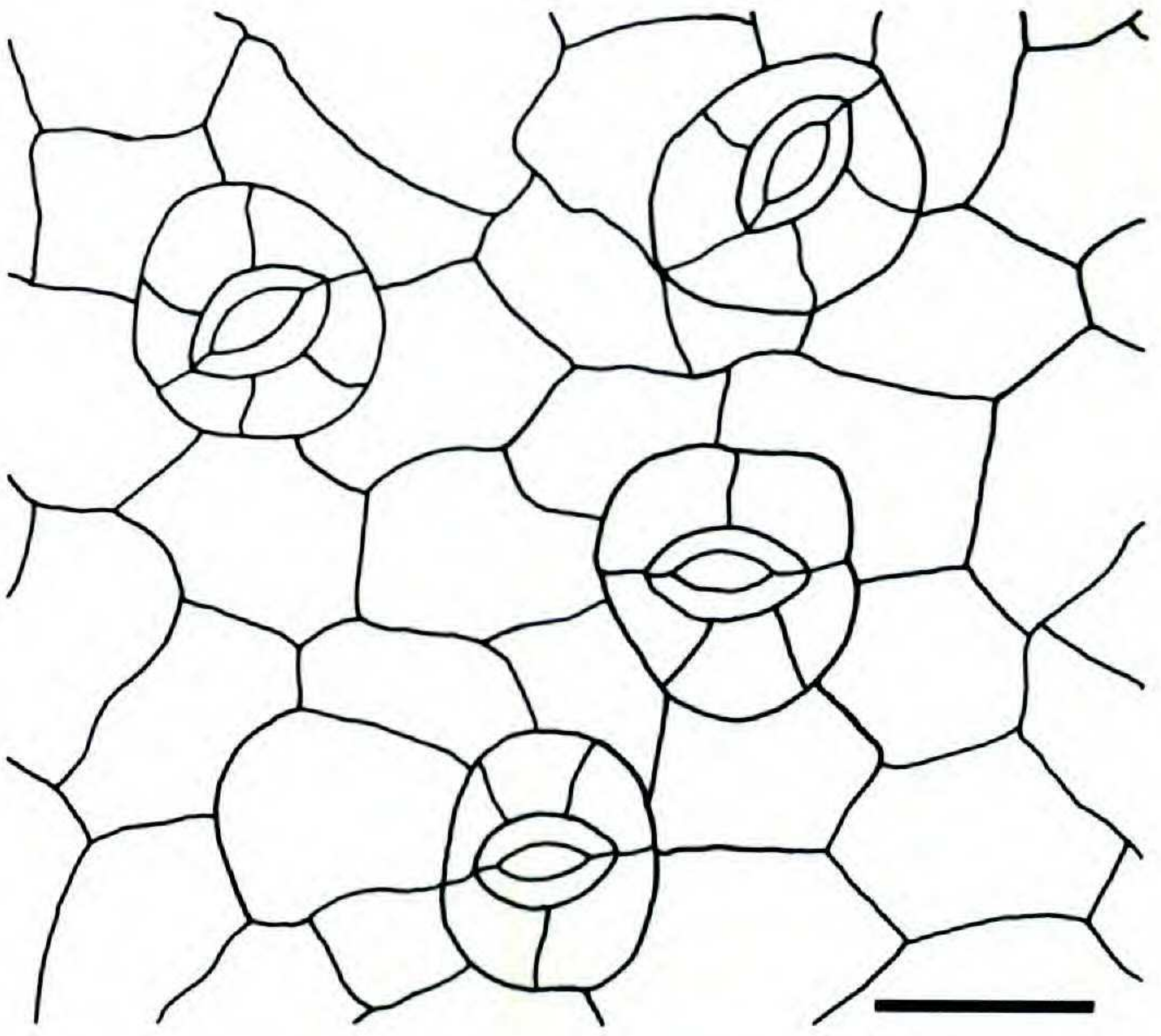


FIGURE 123. Abaxial epidermis of *Paradrypetes ilicifolia*. Bar equals 100 μm.

Paradrypetes, as the name suggests, was considered by Kuhlmann (1935) to be closely related to *Drypetes.* However the foliar morphology of *Paradrypetes,* of which my observations agree with those of Milanez (1935), would make this genus quite anomalous in the Phyllanthoideae and even in the Euphorbiaceae. The most obvious discrepancies are the long, zig-zag intersecondaries, unlike any that I have seen in the subfamily, the tertiaries parallel to the midrib, and the raphides. I have never observed raphides in any phyllanthoides; Gaucher (1902) firmly stated that raphides are never found in the Euphorbiaceae. Milanez (1935) reported that raphides are abundant in every part of the plant, including the embryo. I agree with Webster (1975) that the resemblance between *Paradrypetes* and *Drypetes* is superficial, and that the former should be excluded from the Euphorbiaceae. There are few families with both stipules and raphides (Metcalfe & Chalk, 1950); further study may reveal the proper relationships of this monotypic genus.

RELATIONSHIPS OF THE EUPHORBIACEAE

The foliar morphology of the Phyllanthoideae helps narrow the choice of hypotheses regarding the relationships of the Euphorbiaceae. Particularly significant are the basically theoid teeth of *Bischofia, Drypetes,* and *Putranjiva.* Hayden (1980) reported teeth intermediate between the theoid and violoid types in *Choriceras* (Oldfieldioideae), and Hickey and Wolfe (1975), who presumably examined the uniovulate subfamilies almost exclusively, characterized the Euphorbiaceae as having violoid teeth. This series can be interpreted as a parallel to the shift from theoid to violoid teeth that Hickey and Wolfe (1975) inferred to have occurred in the Violales, supporting the suggestions of Takhtajan (1980) and Thorne (1976) that the two groups share common ancestry.

The Rosidae typically have teeth assigned by Hickey and Wolfe (1975) either to the cunonioid type or its presumed derivative, the rosid type. These types differ from the theoid type in their venation and non-deciduous glandular apex. In contrast, teeth of some Celastrales, particularly members of the Aquifoliaceae and Celastraceae, bear deciduous setae, although these teeth differ from typical theoid teeth in that the former have the apex strongly turned inward toward the sinus whereas the latter are essentially symmetrical. Hickey and Wolfe (1975) originally interpreted the teeth of the Celastrales as modifications of the theoid tooth type, and largely on that basis transferred this order from the Rosidae, in which it is included in the systems of Cronquist (1981) and Takhtajan (1980), to the Dilleniidae. More recently, teeth of the celastroid type have been found in *Brexia* and related genera, which are placed in or near the Saxifragaceae by most authors. Hickey and Wolfe now view the type of tooth found in *Brexia* and the Celastrales as a modification of the similarly asymmetrical cunonioid tooth, and agree that the Celastrales belong in the Rosidae (L. Hickey and J. Wolfe, pers. comm.).

In light of the proposed relationship between the Euphorbiales and the Celastrales, the asymmetrical teeth of *Bischofia* deserve particular attention. Although they, like the teeth of *Brexia* and the Celastrales, have the vein and seta shifted toward the sinus, the degree of shifting is much less than is typical of brexioid/celastroid teeth (Levin, pers. observ.). Tooth morphology, therefore, supports the proposed dilleniid relationships of the Euphorbiaceae somewhat more strongly than the relationship to the Celastrales, but the latter possibility remains. A relationship between Euphorbiaceae and the Geraniales appears much less probable than either of these other possibilities.

Venation patterns provide additional evidence in this regard. In *Drypetes* and many entire-leaved phyllanthoids, the basal secondary veins arise at a significantly different angle from the other secondaries. This pattern suggests either incipient or vestigial actinodromy (Hickey & Wolfe, 1975; Hayden, 1980) and is also found in various primitive Violaceae and Flacourtiaceae (Hickey & Wolfe, 1975). Better developed actinodromy is common in other subfamilies of the Euphorbiaceae, and characterizes a group that Hickey and Wolfe (1975) referred to as the "palmate Dilleniidae," consisting of the Violales, Malvales, and related orders. Although palmate venation occurs sparingly in some rosid orders, including the Geraniales, leaves of the Rosidae typically have pinnate venation and are commonly pinnately compound (Hickey & Wolfe, 1975). Among the Phyllanthoideae (and, in fact, the entire Euphorbiaceae) the only genus with any suggestion of pinnately compound leaves is *Bischofia*.

Thus neither venation nor tooth morphology alone allows the possibility of rosid relationships to be eliminated for the Euphorbiaceae. Taken together, however, these aspects of leaf architecture suggest that the dilleniid relationship is more tenable. The relationship to the Geraniales is unlikely given the theoid teeth of the Phyllanthoideae; although the Celastrales have somewhat similar teeth, differences in the teeth apparent upon close comparison and the suggestion of incipiently actinodromous venation in the Phyllanthoideae make a relationship to this order doubtful. However, the Euphorbiaceae share with the Violales and Malvales both basically similar teeth and venation patterns.

CONCLUSIONS

Leaf architecture and epidermal morphology vary in a taxonomically useful way in the Phyllanthoideae. Most tribes recognized by Webster (1975) appear to be relatively homogeneous and well defined, with most exceptions being tribes that contain genera that have become either herbaceous or highly xerophytic. Within the subfamily (but excluding herbaceous or highly xerophytic genera), venational organization is of lowest rank in those tribes generally agreed to have the most primitive flowers, i.e., the Wielandieae and Amanoeae, and of highest rank in putatively more derived tribes, e.g., Phyllantheae and Hymenocardieae, a pattern that conforms to Hickey's (1971, 1977) generalization that the level of organization increases evolutionarily. Cladistic and phenetic analyses of the foliar morphology presented elsewhere (Levin, 1986 and in press) clarify additional evolutionary patterns, such as the closeness of the Antidesmeae, Aporuseae, and Spondiantheae, and the proximity of *Astrocasia, Andrachne,* and the Phyllantheae.

In addition to confirming the general aspects of Webster's (1975) classification indicated above, foliar morphology indicates some genera whose relationships require reconsideration. Prominent among these are *Celianella, Croizatia, Didymocistus, Jablonskia* (= *Securinega congesta*), and *Neowawraea,* all of which are poorly known and/or recently described. The relationships between *Amanoa* and *Actephila* may also deserve examinaton, because the leaves of these genera differ considerably from each other. Finally, attention should be paid to the suggestion, based primarily on unusual epidermal characteristics but supported by architecture, of a relationship between *Uapaca* and the Aporuseae.

Leaf architecture also proves phylogenetically valuable at higher levels. The presence of theoid teeth and suggestion of vestigial or incipient actinodromy in the most primitive subfamily of the Euphorbiaceae argue for placement of the family in the vicinity of the Violales in the Dilleniidae. The most popular alternative, that of rosid affinities, gains little support from leaf architecture.

LITERATURE CITED

AIRY SHAW, H. K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis's "Dictionary." Kew Bull. 18: 249–273.

———. 1967. Notes on the genus *Bischofia* Bl. (Bischofiaceae). Kew Bull. 21: 327–329.

———. 1973. Willis's A Dictionary of the Flowering Plants and Ferns, 8th edition. Cambridge Univ. Press, Cambridge.

BAILLON, H. 1858. Étude Générale du Groupe des Euphorbiacées. Victor Masson, Paris.

BARANOVA, M. 1972. Systematic anatomy of the leaf epidermis in the Magnoliaceae and some related families. Taxon 21: 447–484.

BEDELL, H. G. 1981. [Abstract:] Leaf architecture and foliar sclereids in Marcgraviaceae (Theales). Publ. Bot. Soc. Amer., Misc. Ser. 160: 62.

BENTHAM, G. 1880. Euphorbiaceae. *In* G. Bentham & J. D. Hooker, Genera Plantarum 3: 239–340. L. Reeve & Co., London.

BHATNAGAR, A. K. & R. N. KAPIL. 1974. *Bischofia javanica*—its relationship with the Euphorbiaceae. Phytomorphology 23: 264–267.

COMYN, J. 1947. Contribution à l'etude anatomique et histologique de la feuille du genre *Uapaca* Baill. (Euphorbiacées). Lille Imp. Morel & Corduant, Paris.

CROIZAT, L. 1940. On the phylogeny of the Euphorbiaceae and some of their presumed allies. Revista Univ. (Santiago) 25: 205–220.

CRONQUIST, A. 1981. An Integrated System of Classification of the Flowering Plants. Columbia Univ. Press, New York.

DAVIS, G. L. 1966. Systematic Embryology of the Angiosperms. John Wiley & Sons, New York.

DEDE, R. A. 1962. Foliar venation patterns in the Rutaceae. Amer. J. Bot. 49: 490–497.

DEN HARTOG, R. M. & P. BAAS. 1978. Epidermal characters of the Celastraceae sensu lato. Acta Bot. Neerl. 27: 355–388.

DILCHER, D. L. 1974. Approaches to the identification of angiosperm leaf remains. Bot. Rev. (Lancaster) 40: 1–157.

DOYLE, J. A. & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac group and their bearing on early angiosperm evolution. Pp. 139–206 *in* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

EHLERINGER, J. & O. BJORKMAN. 1978. Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa.* Oecologia 36: 137–148.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. I. Angiosperms. Chronica Botanica, Stockholm.

FRYNS-CLAESSENS, E. & W. VAN COTTHEM. 1973. A new classification of the ontogenetic types of stomata. Bot. Rev. (Lancaster) 39: 71–138.

GAUCHER, L. 1902. Recherches anatomique sur les Euphorbiacées. Ann. Sci. Nat. Bot., Sér. 8, 15: 161–309.

HAYDEN, W. J. 1980. Systematic anatomy of Oldfieldioideae (Euphorbiaceae). Ph.D. dissertation. Univ. of Maryland, College Park.

——— & D. S. BRANDT. 1984. Wood anatomy and relationships of *Neowawraea* (Euphorbiaceae). Syst. Bot. 9: 458–466.

HICKEY, L. J. 1971. [Abstract:] Evolutionary significance of leaf architectural features in the woody dicots. Amer. J. Bot. 58: 469.

———. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot. 60: 17–33.

———. 1977. Stratigraphy and paleobotany of the Golden Valley formation (early Tertiary) of western North Dakota. Mem. Geol. Soc. Amer. 150: 1–181.

———. 1980. [Abstract:] Leaf architecture of Onagraceae. 2nd Int. Cong. Syst. Evol. Biol., Abstracts, p. 69.

——— & J. A. DOYLE. 1972. [Abstract:] Fossil evidence on evolution of angiosperm leaf venation. Amer. J. Bot. 59: 601.

——— & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

HILL, R. S. 1980. A numerical taxonomic approach to the study of angiosperm leaves. Bot. Gaz. (Crawfordsville) 141: 213–229.

HURUSAWA, I. 1954. Eine nochmalig Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 209–342.

HUTCHINSON, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

JABLONSKY, E. 1915. Euphorbiaceae–Phyllanthoideae–Bridelieae. Pflanzenreich IV, 147-VIII(65): 1–98.

———. 1965. Euphorbiaceae. Pp. 150–178 *in* B. Maguire (editor), The Botany of the Guyana Highland, Part IV. Mem. New York Bot. Gard. 12(3): 1–285.

JUSSIEU, A. DE. 1824. De Euphorbiacearum generibus medicisque earumdem viribus tentamen. Didot, Paris.

KÖHLER, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomy. Grana Palynol. 6: 26–120.

KUHLMANN, J. C. 1935. Novas especies botanicas da Hyléa. Arq. Inst. Biol. Veg. 2: 83–89.

———. 1940. Especies novas equatoriais. Anais Reunião Sul-Amer. Bot. 3: 78–86.

LEVIN, G. A. 1986. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. In press. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis. Syst. Bot.

LUCIC, P. C. 1970. Detailed leaf venation studies of selected species of *Acer*. M.A. thesis. Univ. of California, Berkeley.

MANGENOT, S. & G. MANGENOT. 1958. Deuxième liste de nombres chromosomiques nouveaux chez diverses dicotyledones et monocotyledones d'Afrique occidentale. Bull. Jard. Bot. État 28: 315–329.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons, 2 volumes. Oxford Univ. Press, Oxford.

MILANEZ, F. R. 1935. Anatomia de *Paradrypetes ilicifolia*. Arq. Inst. Biol. Veg. 2: 133–156.

MILLER, K. I. & G. L. WEBSTER. 1966. Chromosome numbers in the Euphorbiaceae. Brittonia 18: 372–379.

MUELLER, J. 1866. Euphorbiaceae [except Euphorbieae]. *In* A. de Candolle (editor), Prodomus Systematis Naturalis Regi Vegetabilis 15(2): 189–1286. Fortin Masson, Paris.

PAYNE, W. W. 1970. Helicocytic and allelocytic stomata: unrecognized patterns in the Dicotyledonae. Amer. J. Bot. 57: 140–147.

———. 1977. A glossary of plant hair terminology. Brittonia 30: 239–255.

———. 1979. Stomatal patterns in embryophytes: their evolution, ontogeny and interpretation. Taxon 28: 117–132.

PAX, F. 1890. Euphorbiaceae. *In* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 1st edition. 3(5): 1–119. Wilhelm Engelmann, Leipzig.

——— & K. HOFFMANN. 1922. Euphorbiaceae–Phyllanthoideae–Phyllantheae. Pflanzenreich IV, 147-XV(81): 1–349.

——— & ———. 1931. Euphorbiaceae. *In* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 2nd edition. 19c: 11–233. Wilehlm Engelmann, Leipzig.

PENZIG, O. & C. CHIABRERA. 1903. Contributo alla conoscenza delle piante acarofile. Malpighia 17: 429–487.

PRAY, T. R. 1953. Morphological and histogenetic studies on the foliar venation of certain angiosperms. Ph.D. dissertation. Univ. of California, Berkeley.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

RAJU, V. S. & P. N. RAO. 1977. Variation in the structure and development of foliar stomata in the Euphorbiaceae. Bot. J. Linn. Soc. 75: 69–97.

RAUNKIAER, C. 1934. The Life Forms of Plants and Statistical Plant Geography. Clarendon Press, Oxford.

ROCK, J. F. 1913. Indigenous Trees of the Hawaiian Islands. Privately published, Honolulu.

ROTHDAUSCHER, H. 1896. Ueber die anatomischen Verhaltnisse von Blatt und Axe der Phyllantheen (mit Auschluss der Euphyllantheen). Bot. Centralbl. 68: 65–79, 97–108, 129–136, 161–169, 193–203, 248–253, 280–285, 305–315, 338–346, 385–393.

RURY, P. M. & W. C. DICKISON. 1977. Leaf venation patterns of the genus *Hibbertia* (Dilleniaceae). J. Arnold Arbor. 58: 209–241.

SEHGAL, O. & G. S. PALIWAL. 1974. Studies on the leaf anatomy of *Euphorbia*. II. Venation patterns. Bot. J. Linn. Soc. 68: 173–208.

SELLING, O. H. 1947. Studies in Hawaiian pollen statistics. II. The pollen of Hawaiian phanaerogams. Special Publ. Bernice Pauahi Bishop Mus. 38: 197–206.

SHARMA, G. K. & B. D. DUNN. 1969. Environmental modification of leaf surface traits in *Datura stramonium*. Canad. J. Bot. 47: 1211–1216.

SHERFF, E. E. 1939. Additional studies of the Hawaiian Euphorbiaceae. Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 547–576.

———. 1942. Some new or otherwise noteworthy Mexican Coreopsideae (genera *Heterosperma* Cav. and *Bidens* C.) and a note on *Xylosma hawaiiense* Seem. Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 570–572.

SMITH, A. C. & E. S. AYENSU. 1964. The identity of the genus *Calyptosepalum* S. Moore. Brittonia 16: 220–227.

STACE, C. A. 1965. Cuticular studies as an aid to plant taxonomy. Bull. Brit. Mus. (Nat. Hist.) Bot. 4: 1–78.

STEYERMARK, J. A. 1952. Botanical exploration in Venezuela—II. Fieldiana, Bot. 28: 243–447.

STONE, B. C. 1967. A review of the endemic genera of Hawaiian plants. Bot. Rev. (Lancaster) 33: 216–259.

TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. (Lancaster) 46: 225–359.

THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35–106.

TUCKER, S. C. 1977. Foliar sclereids in the Magnoliaceae. Bot. J. Linn. Soc. 75: 325–356.

WEBSTER, G. L. 1956. A monographic study of the West Indian species of *Phyllanthus* [Parts 1–3]. J. Arnold Arbor. 37: 91–122, 217–268, 340–359.

———. 1957. A monographic study of the West Indian species of *Phyllanthus* [Parts 4–6]. J. Arnold Arbor. 38: 51–80, 170–198, 295–373.

———. 1958. A monographic study of the West Indian species of *Phyllanthus* [Parts 7, 8]. J. Arnold Arbor. 39: 49–100, 111–212.

———. 1965. A revision of the genus *Meineckia* (Euphorbiaceae). Acta Bot. Neerl. 14: 323–365.

———. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1984a. A revision of *Flueggea* (Euphorbiaceae). Allertonia 3: 259–312.

———. 1984b. *Jablonskia*, a new genus of Euphorbiaceae from South America. Syst. Bot. 9: 129–132.

——— & J. R. Ellis. 1962. Cytotaxonomic studies in the Euphorbiaceae, subtribe Phyllanthinae. Amer. J. Bot. 49: 14–18.

——— & K. I. Miller. 1963. The genus *Reverchonia* (Euphorbiaceae). Rhodora 65: 192–207.

Wolfe, J. A. 1973. Fossil forms of Amentiferae. Brittonia 25: 334–355.